Secondary Succession in Tropical Dry Forests

Drivers and Mechanisms of Forest Regeneration

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Abstract

Secondary succession is a complex process involving numerous factors acting across scales. Understanding secondary succession in tropical dry forests is important for the conservation and restoration of this highly threatened biome. My research aims to improve knowledge of the trajectories and drivers of secondary succession in this biome, and the underlying mechanisms. I used a combination of literature synthesis, observational and experimental approaches to study plant-plant interactions and community changes during succession.

Through review of published studies, I showed that established trees have a mainly positive effect on the seed dispersal, survival and germination of the subsequent generation of woody plants. However, the balance between positive and negative effects is more complex at the seedling establishment stage and can be influenced by the precipitation regime. Meta-analyses of chronosequence studies showed an increase in tree and shrub species richness with succession and a slow convergence of successional forest species composition with that of old-growth forests. Using survey of young woody plants establishing under isolated trees in pastures, I showed that the attributes of the trees influence the functional composition of the regeneration assemblages but are only weakly related to their taxonomic composition. The position of isolated trees in the landscape is also influential, but this is complex and site-specific. Through extensive sampling of leaf functional traits of sapling communities in secondary forests of different successional age, I found that community functional composition shifts from conservative towards acquisitive strategies of resource economics, through both species turnover and intraspecific variation of trait values. Five of the measured traits also showed directional changes with tree ontogeny. Lastly, an experimental test of seed fate showed that leaf litter reduced seed removal in successional forests. Seed germination rate was higher in successional forests compared with open sites and generally benefited from the presence of litter. Overall, this research suggests a higher predictability of successional trajectories when studied through functional rather than taxonomic composition. It also shows heterogeneity in successional trajectories among tropical dry forests that require further study.

Keywords: biodiversity, community assembly, Costa Rica, environmental gradients, facilitation, plant functional traits, regeneration niche

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Contents

List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Derroire, G., Tigabu, M., Odén P.C., Healey, J.R. (2016). The effects of established trees on woody regeneration during secondary succession in tropical dry forests. *Biotropica,* 48(3), pp. 290-300.

II Derroire, G., Balvanera, P., Castellanos-Castro, C., Decocq, G., Kennard, D.K., Lebrija-Trejos, E., Leiva, J.A. , Odén, P.C., Powers, J.S., Rico-Gray, V., Tigabu, M., Healey J.R. (2016). Resilience of tropical dry forests – a meta-analysis of changes in species diversity and composition during secondary succession. *Oikos,* doi: 10.1111/oik.03229.

III Derroire, G., Coe, R., Healey, J.R. (2016). Isolated trees as nuclei of regeneration in tropical pastures: testing the importance of niche-based and landscape factors. *Journal of Vegetation Science*, doi:10.1111/jvs.12404.

IV Derroire, G., Powers, J.S., Hulshof, C.M., Cárdenas Valera, L.E, Healey, J.R. Functional strategies change through species turnover and intraspecific variation in tropical dry forest succession (manuscript under review).

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Preliminary results of a study of the influence of changing abiotic and biotic environmental conditions during succession on the fate of seeds (referred to as the study of seed fate) are also presented and discussed in the thesis.

The contribution of Géraldine Derroire (GD) to the papers included in this thesis was as follows:

I GD reviewed the literature, carried out the analysis and wrote the first version of the paper. All co-authors contributed to editing the paper. GD was responsible for most of the correspondence with the journal, with advice from John Healey (JH). The overall contribution of GD is estimated to be 95%.

II GD designed this study with advice from JH, reviewed the literature, corresponded with authors of published papers to obtain data, carried out the meta-analysis and wrote the first version of the paper. All co-authors contributed to editing the paper. GD was responsible for most of the correspondence with the journal, with advice from JH and input from co-authors. The overall contribution of GD is estimated to be 95%.

III GD designed this study with advice from JH and collected the data with Roberto Espinoza. GD did the statistical analysis with advice from Richard Coe. GD wrote the first version of the paper and all co-authors edited it. GD was responsible for most of the correspondence with the journal, with advice from JH. The overall contribution of GD is estimated to be 95%.

IV GD designed the study with advice from JH, Jennifer Powers and Catherine Hulshof. GD was responsible for data collection with help from Luis Cárdenas Valera, Daniel Perez Aviles, Christina Smith and Erick Calderon Morales. GD carried out the chemical analyses and the statistical analysis. GD wrote the first version of the paper and all co-authors edited it. The overall contribution of GD is estimated to be 95%.

Abbreviations

ACG	*Área de Conservación de Guanacaste*
AIC	Akaike information criterion
ANOVA	Analysis of variance
DBH	Diameter at breast height
FAO	Food and agriculture organisation
FRA	Global forest resources assessment
GLM	Generalised linear model
LA	Leaf area
LCC	Leaf carbon concentration
LDMC	Leaf dry matter content
LNC	Leaf nitrogen concentration
LPC	Leaf phosphorous concentration
PCA	Principal component analysis
PIC	Phylogenetically independent contrast
RDA	Redundancy analysis
SLA	Specific leaf area

1 Introduction

1.1 Importance of tropical secondary forests

Most of the tropical forests of the future are expected to be “secondary forests regenerating after previous clearing” (Wright & Muller-Landau, 2006). The current extent of tropical secondary forests is difficult to estimate, partly because of differences in definition of secondary forest. For the Global Forest Resources Assessment (FRA), the Food and Agriculture Organisation of the United Nations (FAO) uses the designation of “other naturally regenerating forest” for any non-planted forests with clear “visible signs of past or present human activity” (FAO, 2010). The FRA 2010 estimated that these forests account for 57% of the world’s total forest area (FAO, 2010), and more than 80% of the tropical countries that provided data reported an area of “other naturally regenerating forests” exceeding that of primary forest (Chazdon, 2014). However, the definition used by the FAO is broad: it encompasses both degraded forests (after logging activity for instance) and forests re-establishing after another land use, two types of forests differing greatly in their structure, composition and dynamics (Putz & Redford, 2010; Chazdon, 2014). For the present study, I use “secondary forests” to refer exclusively to forests establishing after previous deforestation (Wright & Muller-Landau, 2006; Putz & Redford, 2010), which Chazdon (2014) prefers to call “second-growth” or “regenerating forests” to avoid ambiguity. To refer to forests with no signs of human activity, I prefer the more neutral term of “old-growth forests” to the terms “mature forests”, “primary forests” or “pristine forests”.

Because of the importance of their current and estimated future extent, it is important to understand the ecology of tropical secondary forests and their potential for biodiversity conservation and provision of ecosystem services. Secondary forests have an important role to play for the provision of regulating and supporting ecosystem services[1]. They have a high capacity for carbon sequestration in biomass: Martin *et al.* (2013) estimated that tropical

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[1] as defined by the Millennium Ecosystem Assessment (2003)

secondary forests can recover 83% the aboveground biomass stock of old-growth forest in 85 years (based on 326 secondary forest plots) and Poorter *et al.* (2016) estimated that neotropical secondary forests can recover 90% in an average of 66 years (based on 28 forest sites). Poorter *et al.* (2016) also found that the average aboveground carbon uptake rate over the first 20 years was 11 times that of old-growth forests (based on 44 sites). Belowground biomass stock seems to be slower to recover: Martin *et al.* (2013) found that it reaches only 50% of the stock of old-growth forests after 80 years (based on 76 plots). Trends for soil carbon are less clear: Martin found a very weak correlation between soil carbon and successional age, with soil carbon stocks in secondary forests similar to those in old-growth forests (185 plots), whereas Don *et al.* (2011) estimated that secondary forests store 9% less carbon in their soil than old-growth forests, using a definition of secondary forest that includes managed and partially exploited forests (71 studies). Although the provision of other ecological services has been less studied and not quantitatively synthesised, Chazdon (2014) reviewed evidence of their importance for many hydrological functions (such as evapotranspiration) and nitrogen fixation.

For biodiversity, several quantitative reviews show the capacity of secondary forests to recover levels of richness of animal and plant species similar to those of old-growth forests within a few decades. On the basis of 39 studies considering mainly insects and vertebrates, Dunn (2004) found that the animal species richness of tropical secondary forests can reach that of old-growth forests after two to four decades. Martin *et al.* (2013) estimated this recovery time to be five decades for tree species (based on 204 secondary forest plots) and to be more than a century for epiphyte species (based on 65 secondary forest plots). The rates of recovery of animal and plant species composition are however slower than species richness (Dunn, 2004; Martin *et al.*, 2013). Reviewing 65 studies, Dent and Wright (2009) showed that many animal species of old-growth forests can colonize secondary forests, but some highly specialised ones do not. These results, together with the predictions of Wright and Muller-Landau (2006) for future forest cover, support the potential of secondary forests to mitigate species extinction due to deforestation but suggest that secondary forests cannot fully replace old-growth in term of biodiversity conservation (Chazdon, 2014).

1.2 Secondary succession in tropical forests

1.2.1 Models of forest succession: determinism and stochasticity

Succession has been a major focus of plant community ecology for more than a century (McIntosh, 1999), yet the processes underlying assembly of secondary forests continue to be actively researched (Norden *et al.*, 2015). The early view of Clements (1916) of deterministic and convergent succession towards a single state of equilibrium (monoclimax hypothesis), was highly holistic (Finegan, 1984) and drew an analogy between the development of an ecosystem and that of an organism. The relay floristics model (Egler, 1954), close to Clements' view, describes a successive replacement of species during succession, based on facilitation of the establishment of later successional species by earlier ones (facilitation model of Connell and Slatyer (1977). Other more individualistic and reductionist models consider that all groups of species are present from the beginning of succession and successively assume dominance (the initial floristic composition model of Egler (1954): either species of late succession become dominant by tolerating environmental conditions in which early successional species cannot survive (tolerance model of Connell and Slatyer (1977), or species dominant earlier in succession inhibit the establishment of later ones (inhibition model of Connell and Slatyer (1977) leading to "arrested succession". These deterministic models are all based on the idea that trade-offs between plant traits promote success in different stages of succession (Huston & Smith, 1987). The deterministic character of succession was challenged as early as the 1920s by Gleason (1926) who introduced the notion of unpredictability. Lawton (1987) proposed a model of succession based only on random survival of established species and colonisation by new species, paving the way for the neutral theory of community assembly (Hubbell, 2001). Although deterministic niche-based and neutral models have often been treated as mutually exclusive explanations for observed patterns of succession, a growing body of literature shows the importance of the integration of the two (Chave, 2004; Tilman, 2004; Gravel *et al.*, 2006; Norden *et al.*, 2015). The alternative stable states model combines elements of both: it states that an ecosystem can follow one of several possible successional trajectories, depending on past events and the timing of arrivals of organisms combined to some random events (Young *et al.*, 2001; Temperton & Hobbs, 2004). However, its general applicability to forest ecosystems has recently been challenged (Newton & Cantarello, 2015).

Moving away from the opposition between deterministic and neutral models of succession, the focus of research has shifted towards understanding the relative contribution of deterministic events and stochastic ones (Norden *et al.*, 2015) and assessing the factors affecting successional trajectories (Chazdon, 2003). The aim is now to understand if, and under what circumstances, secondary communities converge towards the state of the vegetation before disturbance or lead to alternative stable states (Young *et al.*, 2005; Norden *et al.*, 2009).

I therefore define forest succession as the set of changes (in structure, composition and functioning) occurring in an entire forest following a previous non-forested state, without making an *a priori* inference about its predictability. I focus on secondary succession, the form of succession that occurs on land where legacies of the previous ecosystem (such as soil or propagules) are still present, as opposed to primary succession (Chazdon, 2003). Forest re-establishing on land previously used for agricultural activities is the most common type of successional forests in the tropics (Chazdon *et al.*, 2007).

1.2.2 Factors influencing secondary succession in tropical forests

In this section, I present the multiple interacting factors that influence successional trajectories in tropical forests, at scales ranging from the region to the community. They first affect the early stages of succession, which in turn modify biotic and abiotic conditions for the later stages, and therefore have long-term effect on secondary forests (Figure 1). I provide examples from both wet and dry tropical forests (the distinct characteristics of tropical dry forests are highlighted in section 1.5).

Abiotic environmental factors

Several abiotic environmental factors can influence trajectories of secondary succession at scales ranging from the region to the site. The climate of the region affects successional trajectories: quantitative reviews have shown that precipitation regime affects the rate of aboveground biomass recovery (Becknell *et al.*, 2012; Poorter *et al.*, 2016) and the relative importance of vegetative *versus* seed reproduction (McDonald *et al.*, 2010). Soil properties of the site can affect the structure, dynamics, and species richness and composition of successional forests (Gehring *et al.*; Finegan & Delgado, 2000; Ceccon *et al.*, 2003; Ceccon *et al.*, 2004; Powers *et al.*, 2009).

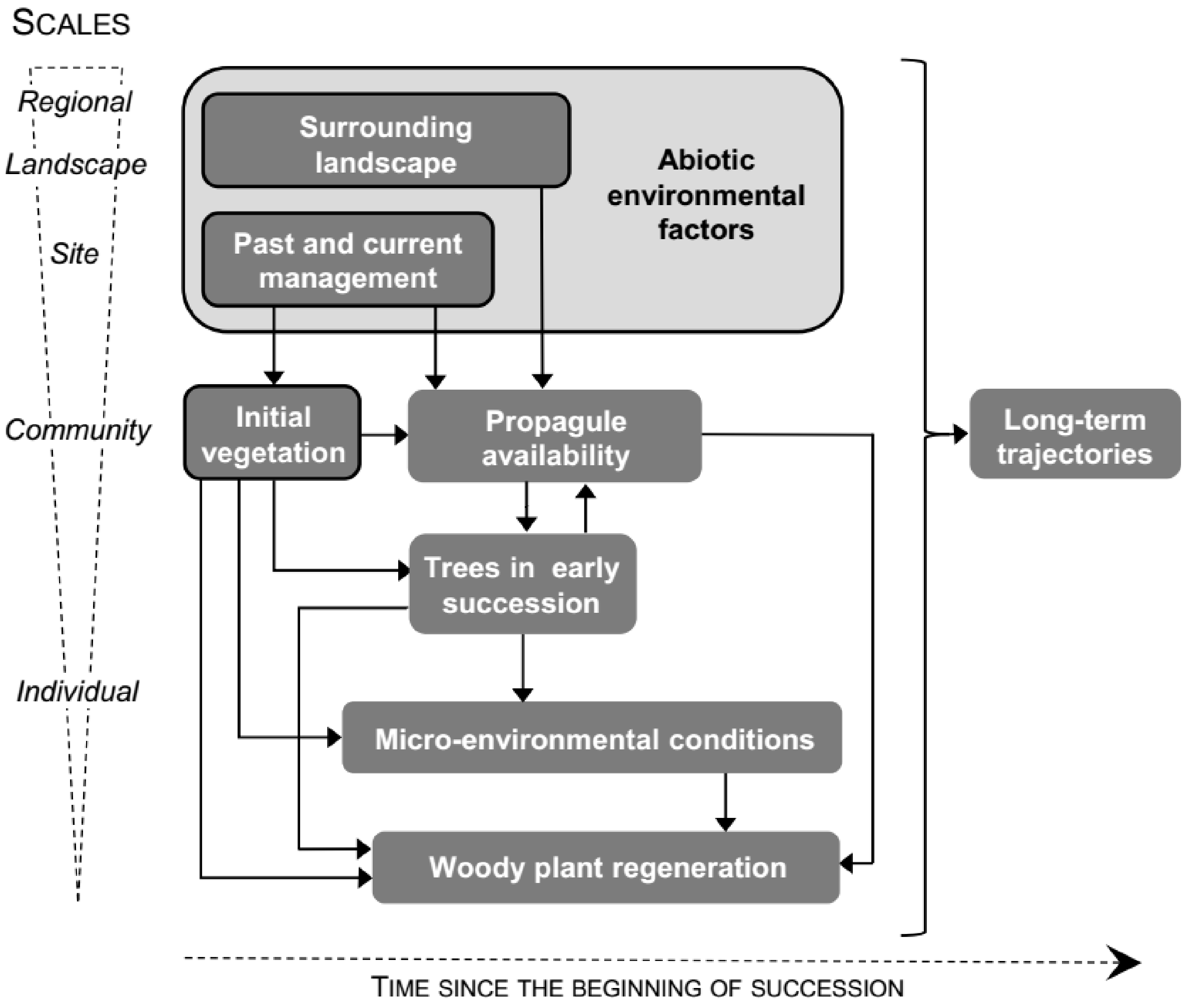

Figure 1. Conceptual framework of the factors influencing succession in tropical forests. Surrounding landscape and past and present management are not considered to be abiotic environmental factors but they act at spatial and temporal scales that partially overlap with these. Boxes encircled by a black line are the factors acting from the beginning of succession (discussed in this section).

Surrounding landscape

The composition of the surrounding landscape is important: nearby forests (old-growth forests and riparian vegetation) act as a source of seeds that can colonize the successional site (Chazdon, 2014). The distance to the nearest forest and area of forest in the landscape influences the structure and species diversity (Slocum & Horvitz, 2000; Griscom *et al.*, 2009; Sovu *et al.*, 2009; Duarte *et al.*, 2010; Gomes Reis Lopes *et al.*, 2012). The direction of the forest relative to the dominant winds can also affect the relative proportion of seeds with different dispersal syndromes dispersed into successional forests (Janzen, 2002; Castillo-Nunez *et al.*, 2011). Scattered trees and live-fences improve seed dispersal in the landscape by acting as stepping stones and corridors for animal dispersers (Estrada *et al.*, 1993; Chazdon *et al.*, 2011).

Past and current management

Past and current management affects successional trajectories. The type of land use before its abandonment has an effect on the structure and rate of biomass accumulation, the species richness and composition, and the relative proportion of dispersal syndromes of the plants in successional forests (Ferguson *et al.*, 2003; Larkin *et al.*, 2012; Martin *et al.*, 2013). This is due to several reasons: different past land uses have different impact on the soil (*e.g.* compaction, erosion, fertility) (Maass *et al.*, 1988; De Wilde *et al.*, 2012). The vegetation present at the time of abandonment also differs between past land uses (this point is developed in the next paragraph). The duration and intensity of the previous land use are also important factors (Pereira *et al.*, 2003; Sovu *et al.*, 2009). Fire, used for management purposes or accidental, occurring before or after the abandonment of the previous land use decreases species richness and changes the species composition by favouring fire-tolerant species and species capable of resprouting (Rico-Gray & Garcia-Franco, 1992; Marod *et al.*, 2002; Hooper *et al.*, 2004). When fire is especially intense it can severely reduce regeneration by destroying the soil seed bank and killing roots (Kennard *et al.*, 2002). Grazing occurring in successional forests decreases biomass and species accumulation (Griscom *et al.*, 2009), alters species composition (Stern *et al.*, 2002) and can also have the beneficial effect of grass control (Blackmore & Vitousek, 2000; Janzen, 2002; Stern *et al.*, 2002; Larkin *et al.*, 2012). Lastly, restoration activities also affect successional trajectories (see section 1.6).

Initial vegetation

The vegetation *in situ* at the beginning of succession influences the establishment of woody vegetation. Grasses, and especially highly productive exotic species planted in pasture sites, have an overall negative effect on the regeneration of woody plants. Because of their high seed dormancy capacity, some herbaceous species can remain dominant in the soil seed bank a long time after the beginning of succession (Martins & Engel, 2007; Maza-Villalobos *et al.*, 2011b). In many cases, grass reduces or removes the capacity of woody species to establish by competing with them for resources (Cabin *et al.*, 2000; Cabin *et al.*, 2002b; Ferguson *et al.*, 2003; Hooper, 2008; Griscom *et al.*, 2009; Thaxton *et al.*, 2012; Wolfe & Van Bloem, 2012). Moreover, grass is a highly combustible fuel biomass and can increase the risk of fire incidence and its intensity (D'Antonio & Vitousek, 1992; Blackmore & Vitousek, 2000). However, in some cases, grasses can provide suitable conditions for woody species establishment (Hardwick *et al.*, 1997; Esquivel *et al.*, 2008). Woody vegetation present at the beginning of succession, such as isolated trees in pastures and remnant trees in land under shifting cultivation, can enhance regeneration of woody species (Guevara *et al.*, 1992; Carrière *et al.*, 2002b; Schlawin & Zahawi, 2008) through resprouting (Kammesheidt, 1999; Sampaio, 2007), input of seeds (directly or through attraction of animal dispersers) (Guevara *et al.*, 1986; Slocum & Horvitz, 2000; Carrière *et al.*, 2002a; Chazdon, 2014) and amelioration of microclimate (Duarte *et al.*, 2010). Remnant trees can have long-lasting effects (at least 20 years after beginning of succession) on the species diversity and composition of secondary forests through their impact on the regeneration process (Sandor & Chazdon, 2014).

1.3 Importance of plant-plant interactions for succession

In this section, I present the different types of plant-plant interactions and explain their importance for succession. I do not review empirical evidence of plant-plant interactions during succession as this is done for tropical dry forests in paper I and summarised in section 4.1.

1.3.1 Types of plant-plant interactions

Plant-plant interactions are processes by which a plant influences the establishment and fitness of other plants, positively (facilitation) or negatively (competition). They can have an effect on ecological processes and patterns from the individual to the landscape scale (Bruno *et al.*, 2003), and are therefore important in structuring plant populations and communities (Bertness & Callaway, 1994).

Competitive interactions have been much more studied yet facilitative interactions have received increasing interest since the 1990s (Michalet & Pugnaire, 2016). Facilitation and competition often co-occur in the same community and the balance between these processes is complex (Callaway & Walker, 1997). It can depend on the intensity of abiotic constraints: Grime (1979) suggested that competition was more important in high productivity environments. Conversely Bertness and Callaway (1994) made the hypothesis that facilitation was more important in environments with high abiotic stress or high consumer pressure. This hypothesis, called the stress gradient hypothesis, has been supported by a number of meta-analyses (*e.g.* Lortie and Callaway 2006; He *et al.* 2013) but challenged by other studies (Maestre *et al.*, 2005; Soliveres & Maestre, 2014; Butterfield *et al.*, 2016), and empirical evidence suggests that beyond a threshold of harshness of environmental conditions competition can overtake facilitation and result in a negative net effect on plant performance

(Maestre & Cortina, 2004; Siles *et al.*, 2010). The outcome of plant-plant interactions can also depend on the life stages (Callaway & Walker, 1997): suitable conditions for the younger stages of a plant's regeneration cycle can be unsuitable for its adult stage (Grubb, 1977) and the outcome of plant-plant interactions can change from facilitative to competitive during the life of a plant. Finally, Ganade *et al.* (2008) suggest that there can be an interplay of the stress gradient hypothesis and the effect of life stage.

Another way of looking at plant-plant interactions is to consider the mechanisms underlying them. Direct interactions happen through modification of the abiotic environment (light, temperature, soil moisture, chemical or physical properties) whereas indirect interactions happen through a third organism (*e.g.* herbivore, pollinator, seed disperser, mycorrhizal fungus or soil microbe) (Callaway, 1995; Bruno *et al.*, 2003; Callaway, 2007).

1.3.2 Core processes for deterministic niche-based models of succession

Plant-plant interactions are central to deterministic niche-based models of succession. The model of Clements (1916) and the facilitation model of Connell and Slatyer (1977) are based on an amelioration of environmental conditions by early successional species (*i.e.* species that establish and dominate at early stages of succession) for late successional species, whereas the tolerance and inhibition models (Connell & Slatyer, 1977) are based on negative interactions. The realised niche is often viewed as the set of environmental conditions in which a species can establish, considering biotic interactions with other species (Bruno *et al.*, 2003). Facilitation can therefore result in an expansion of the realised niche and competition in a reduction (Bruno *et al.*, 2003; Callaway, 2007; Bulleri *et al.*, 2016).

The nurse plant effect, defined as facilitation of the recruitment of plants under the canopy of other plants (Callaway & Walker, 1997; Rodríguez-Echeverría *et al.*, 2016), is commonly observed during succession in tropical forests. Shrubs, such as the nitrogen fixing *Leucaena leucocephala* in Puerto Rico (Molina Colon & Lugo, 2006; Santiago-Garcia *et al.*, 2008; Wolfe & Van Bloem, 2012) and *Chromolaena odorata* in West Africa (Kassi N'Dja & Decocq, 2008), or trees, such as several species of *Mimosa* or *Guazuma ulmifolia* in Mesoamerica (Romero-Duque *et al.*, 2007; Lebrija-Trejos *et al.*, 2008; Williams-Linera *et al.*, 2011), can facilitate the establishment of other species under their cover. On the other hand, the inhibition of woody species by grass after abandonments of pasture sites (described in section 1.2.2) is an example of negative interactions.

1.4 Species-based and functional trait-based approaches

1.4.1 From context-specific accuracy to global comparisons

The taxonomic approach, giving a central role to the species, has long been the main approach adopted in community ecology (McGill *et al.*, 2006). This approach focusses on species-specific requirement and pairwise interactions between species (McGill *et al.*, 2006). It is particularly valuable for conservation, restoration and management. It allows emphasis to be placed on species that are seen as having high conservation value, such as highly threatened (IUCN, 2015) or emblematic species (Clark & May, 2002; Sergio *et al.*, 2006), identification of geographical priorities for conservation (Myers *et al.*, 2000; Jenkins *et al.*, 2013) and guiding of management practices (such as species choice by practitioners). However, the species-based approach has several limitations. (1) It relies on the assumption that the species level is the most appropriate level to understand plant ecology, in other words that most of the variation of traits related to plant fitness and function is greater between species. This is challenged by the hypothesis of phylogenetic conservatism suggesting that higher taxonomic levels can be more relevant (Ackerly, 1999), and by an increasing number of studies showing substantial variation in trait values within species (this point is detailed in section 1.4.3). (2) The species-based approach reaches its limits of practicality in species rich ecosystems, such as tropical forests. (3) The highly context-specific and locally-contingent understanding of ecological processes resulting from this approach impedes comparison between sites and assessment of general patterns of community assembly and functioning (Duarte *et al.*, 1995; Simberloff, 2004; McGill *et al.*, 2006).

Non-taxonomic approaches are based on the idea that species are not functionally unique entities (Duarte *et al.*, 1995). Using the characteristics of plants, rather than their taxonomic identity, to classify them and understand their function is not a new approach (Garnier *et al.*, 2016). This approach has developed over the last century, notably with the work of Raunkiaer (1934), Grime (1979) and Noble and Slatyer (1980) and has gained momentum in the last two decades with the increasing number of studies based on functional traits[2]. Functional traits are defined as “any morphological, physiological or phenological feature measurable at the individual level” (Violle *et al.*, 2007) and relate to the function and fitness of organisms (Lavorel & Garnier, 2002; McGill *et al.*, 2006; Violle *et al.*, 2007). They can provide mechanistic answers to questions ranging from the individual and population scales, such as

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[2] See the post of Brian McGill on the blog *Dynamic ecology* (https://dynamicecology.wordpress.com/2015/07/01/steering-the-trait-bandwagon/)

those relating to predicting the performance and fitness of plants (Reich *et al.*, 2003; Wright *et al.*, 2010), to the ecosystem scale, such as assessing ecosystem functioning (Tilman *et al.*, 1997; Diaz & Cabido, 2001; Lavorel & Garnier, 2002) and services (Diaz *et al.*, 2007). At the community scale, the functional trait-based approach provides information about community assembly. Mean trait values can be used to understand how environmental gradients structure plant communities (Lohbeck *et al.*, 2013; Fortunel *et al.*, 2014). Characteristics of the distribution of traits in a community can help in assessing the importance of abiotic environmental filtering (expected to produce under-dispersed trait distribution), and competition, leading to niche differentiation between species (hypothesis of "limiting similarity", expected to produce over-dispersed trait distribution) (Chesson, 2000; Cornwell *et al.*, 2006). However, competition can also result in under-dispersed trait distribution (as does abiotic environmental filtering) through "equalizing mechanisms" (Chesson, 2000). Consideration of different types of traits (resource acquisition traits *versus* regeneration traits) and the types of null model used to test hypotheses can help distinguish between these different mechanisms (Grime, 2006; Bernard-Verdier *et al.*, 2012).

By providing an approach based on a limited number of traits, as an alternative to a high number of species, the functional trait approach reduces the dimensionality and complexity of plant communities (McNamara *et al.*, 2012; Laughlin, 2014). Furthermore, most traits can be measured in any plants worldwide while the set of species present in a community is dependent on the local species pool. As a result, the great value of the trait-based approach is the potential for global comparisons to determine which trends of plant community responses to, and effects on, their environment are common among plant communities globally, and which are more locally specific (Duarte *et al.*, 1995; Reich *et al.*, 1997; McGill *et al.*, 2006).

1.4.2 Functional traits and plant strategies

The identification of plant strategies which summarise the capacity of plant species to establish and reproduce in a given environment (Grime, 1979), is an approach to using functional traits that further reduces dimensionality (Laughlin, 2014). Discrete classifications of species according to their resource requirements, such as guilds (Root, 1967) and functional groups (Cummins, 1974), have progressively lost their importance with the increasing emphasis on continuous spectra of strategies (Laughlin, 2014). In the framework of Grime (1979), species' strategies are located inside a triangle with its three corners being competitive, stress-tolerance and ruderal strategies respectively (the "C-S-R triangle theory").

The exact position of a species in the triangle is defined by its traits and corresponds to its relative tendency to fit each of these strategies; “generalist” species are located in the centre.

The exploration of correlations among functional traits allows the identification of the main axes defining the patterns of trait variations and, potentially, the trade-off between strategies (Laughlin, 2014). Westoby (1998) proposed a three dimensional scheme based on just three functional traits: specific leaf area (SLA), height of the plant at maturity and seed mass (the “LHS” scheme). These traits represent three main axes of trait variation termed: resource economics, stature and regeneration (Garnier *et al.*, 2016). In a recent study on the largest sample of plant species ever analysed, Díaz *et al.* (2016) considered six important traits related to growth, survival and regeneration and showed that most of their variation was accounted for by just two axes: the first being defined by plant and propagule sizes (with short species tending to have small propagules) and the second related to leaf resource economics (explained below). Although the intrinsic number of axes of variation in functional traits remains an open question, Laughlin (2014) found it to be higher than the three proposed by Westoby (1998). Laughlin (2014) used a variety of methods to estimate dimensionality of three different datasets and found that their median dimensionality ranged between four and six. He recommends the use of traits of several organs and the consideration of additional types of traits, such a phenological and life-history traits.

The axis of trait variation that has been developed and tested with most empirical evidence is that of leaf resource economics. This is the axis that I focus on in paper IV. Wright *et al.* (2004) showed the evidence for a main axis of leaf functional traits across plants worldwide, which has been called the leaf economics spectrum. At one end of this spectrum are productive strategies with a fast return on investment of resources in leaves characterized by high leaf nutrient concentrations, high metabolic rates and short leaf lifespan, also called acquisitive strategies (Reich, 2014). At the other end, conservative strategies, with a slow return on investment, are characterized by low metabolic rates, and expensive leaf construction and defence costs allowing a longer leaf lifespan. There is also evidence for one main axis representing variation in such economics strategies for other plant organs: stems (Reich *et al.*, 2003; Chave *et al.*, 2009) and roots (Prieto *et al.*, 2015; Roumet *et al.*, 2016). Reich (2014) propose the integration of the economics spectra of organs into a whole-plant economics spectrum defined by the variation between slow/conservative and fast/acquisitive strategies, although empirical results show decoupling of these spectra (Baraloto *et al.*, 2010b). In line with the hypothesis of Grime (1979) that there is a positive correlation of the capacities of a species to acquire different resources, Reich (2014) provides evidences for the association of these spectra with all resources gradients (light, water, nutrients); acquisitive strategies being advantageous in high resource environments and conservative strategies enhancing survival in low resource environments.

1.4.3 Variation of functional trait values within and among species

Although functional traits are defined as features measured at the scale of individuals (Violle *et al.*, 2007), most functional trait-based studies in community ecology overlook the variation in trait values occurring within species (Violle *et al.*, 2012), following the idea that "to be useful to community ecology, traits should vary more between than within species" (McGill *et al.*, 2006). Standard protocols recommend sampling a limited number of individuals per species in standardised environmental conditions (Cornelissen *et al.*, 2003; Perez-Harguindeguy *et al.*, 2013) and calculating a mean value per species from these which is used to calculate functional diversity indices of communities (Laliberte & Legendre, 2010; Mouchet *et al.*, 2010). However, this approach is increasingly challenged and there is growing recognition of the importance of intraspecific variation of functional trait values (Lepš *et al.*, 2011; Violle *et al.*, 2012; Laughlin & Messier, 2015).

Several studies have shown that variation of trait values within species is not negligible compared with variation between species. Siefert *et al.* (2015) carried out a meta-analysis of 629 plant communities worldwide for 36 functional traits and showed that intraspecific variation accounted for an average of 25% of the total trait variation within communities and 32% of the total trait variation across communities. For tropical forests, Messier *et al.* (2010) and Hulshof and Swenson (2010) partitioned the variance of trait values for commonly measured leaf functional traits across nested scales[3]. Messier *et al.* (2010) found that intraspecific variance accounted for 48% of the total variance of trait values for SLA and leaf dry matter content (LDMC), and Hulshof and Swenson (2010) found that the contribution of intraspecific variance ranged from 35 to 68% of the total variation (for leaf area, dry mass, SLA and leaf water content).

Intraspecific variation of functional trait values can result from both the genetic variation between individuals and the capacity of a genotype to express different phenotypes (Violle *et al.*, 2012; Garnier *et al.*, 2016). The latter can occur as a response to variation in environmental conditions in space or in time (*e.g.* between seasons, Gotsch *et al.*, 2010) (Violle *et al.*, 2012), which is called phenotypic plasticity (Valladares *et al.*, 2006). Genetic

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[3] *N.B.* The results of such studies partitioning the variance of trait values across scales are highly dependent on methodological choices (sampling design and number and order of nested levels considered) (Messier *et al.*, 2010) and therefore need to be compared with caution.

variability and phenotypic plasticity are difficult to disentangle without experimental studies, but doing so is not essential for community studies because both mechanisms can be a response to environmental conditions (Violle *et al.*, 2012), although over different time scales (natural selection by past conditions over a long evolutionary time scale for genetic variability and changes at the scale of the life of an individual for phenotypic plasticity). The phenotypes expressed by a given genotype can also change with the development of a plant (ontogeny) (Thomas & Winner, 2002; Niklas & Cobb, 2008; Spasojevic *et al.*, 2014).

The importance of considering intraspecific variation for studies of community ecology is supported by both theoretical arguments and empirical evidence. Treating species' functional trait values as discrete single values (*e.g.* by using species mean value) gives average information on the environmental requirements of species (Violle *et al.*, 2012). Considering it as the within-species distribution (*i.e.* the distribution of trait values measured on different individuals of the same species) provides information on a species' capacity to establish and thrive in different conditions of resource availability and interactions with neighbouring plants (Violle *et al.*, 2012; Laughlin & Messier, 2015). This latter approach provides a better assessment of the niche of a species, which is important in community ecology to understand mechanisms of species coexistence and community assembly. Including intraspecific variation of functional trait values can therefore provide a better understanding of abiotic and biotic drivers of community assembly (Violle *et al.*, 2012). This is supported by empirical evidence: several studies have shown that intraspecific variation can be important in explaining community variation along environmental gradients (*e.g.* Lepš *et al.* 2011; Carlucci *et al.* 2015). Furthermore, observed patterns in interspecific variation, such as trait correlations (Laughlin & Messier, 2015) or direction of change along environmental gradients (Albert *et al.*, 2010; Lepš *et al.*, 2011; Kichenin *et al.*, 2013), do not necessarily hold for intraspecific variation. These are reasons in favour of a change from a species-based to an individual-based approach to community ecology. Ultimately this could lead to species identity having a much diminished importance (Messier *et al.*, 2010). However, there are good theoretical and empirical reasons for considering both interspecific and intraspecific variation, which is the approach I use for paper IV. (1) Phylogenetic conservatism of trait values predicts that individuals that are phylogenetically close should have close trait values, therefore it supports the importance of the species and higher phylogenetic levels (Ackerly, 1999). (2) Many studies show that the interspecific level is the one where the highest variation is found (*e.g.* Markesteijn *et al.* 2007; Hulshof and Swenson 2010; Powers and Tiffin 2010). (3) A sampling approach based solely on individuals would require the measurement of traits on all individuals in a community (Violle *et al.*, 2012), which is difficult in practice. It is important to move from the use of a single trait value per species across all communities to a separate value per species per community (Baraloto *et al.*, 2010a; Lepš *et al.*, 2011). At present there is an urgent need for studies that identify the circumstances under which it is important to consider intraspecific variation, such as that of Spasojevic *et al.* (2016).

1.5 Tropical dry forests

1.5.1 Definitions, distribution and state of conservation

There are several definitions of tropical dry forests. Mooney *et al.* (1995) merely define tropical dry forests as "forests occurring in tropical regions where there are several months of severe, even absolute, drought". Most definitions are based on a range of mean annual precipitation, *e.g.* 250-2000 mm (Murphy & Lugo, 1986), 400-1700 mm (Gerhardt & Hytteborn, 1992), 500-2000 mm (Holdridge, 1967; Becknell *et al.*, 2012) or 700-2000 mm (Sanchez-Azofeifa *et al.*, 2005), and some definitions also use a minimum mean annual temperature, 17 °C (Holdridge, 1967) or 25 °C (Sanchez-Azofeifa *et al.*, 2005). As well as these two, Holdridge (1967) based his definition on a third variable, the annual ratio of potential evapotranspiration to precipitation (> 1). Other definitions consider a minimum number of dry months[4], *e.g.* three (Sanchez-Azofeifa *et al.*, 2005), four (Becknell *et al.*, 2012) or ~ six (Gerhardt & Hytteborn, 1992). For the present study, I define tropical dry forests as forests with a mean annual precipitation of 500-2000 mm, a mean annual temperature > 17 °C and at least three dry months (monthly precipitation < 100 mm).

Although the seasonality of precipitation is a major environmental factor affecting the ecological processes of both tropical dry forests and savannas, they are distinct vegetation types differing in their structure and ecology (Dexter *et al.*, 2015; Veenendaal *et al.*, 2015). In the Neotropics, they also have distinct floristic compositions (Pérez-García & Meave, 2006; Dexter *et al.*, 2015). While tropical dry forests are dominated by trees, and have a relatively closed canopy and a higher aboveground biomass, savannas are more open and are characterised by the presence of an abundant grass layer (Pennington *et al.*, 2000; Pennington *et al.*, 2006; Pennington *et al.*, 2009; Veenendaal *et al.*, 2015), usually of species with a C4 photosynthetic pathway (Dexter *et al.*, 2015). Tropical dry forests and savannas can occur under similar climatic conditions and therefore often co-exist in the same area (Pennington *et*

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[4] There is generally no precipitation during the dry months. Many definitions of tropical dry forests do not specify a definition of dry month. Sanchez-Azofeifa *et al.* (2005) define it as a month with < 100 mm precipitation.

al., 2006; Pennington *et al.*, 2009). Their structural and floristic differences are, however, the results of distinct environmental drivers that have shaped the evolution of their distinct floristic assemblages (Furley, 2007). Fire is considered to be the major environmental factor responsible for the differences in the ecology of these two vegetation types: while natural fire is an essential part of the ecology of savannas, tropical dry forests usually do not experience fire, except when caused by human activities (Hughes *et al.*, 2013; Dexter *et al.*, 2015). As a consequence of their different environmental drivers, forest and savanna plant species have different sets of trait values. Savanna species are generally more tolerant of fire due to adaptions such as thick and corky bark, protected buds, and large investment in carbohydrate reserves and high root biomass allowing them to quickly resprout after a fire. In contrast, forest species usually lack these adaptations but have a faster growth rate enhancing their competitiveness in the denser forest environment, as well as the ability to regenerate under a closed canopy (Hoffmann, 2000; Pennington *et al.*, 2000; Furley, 2007; Pennington *et al.*, 2009; Hoffmann *et al.*, 2012).

A number of studies have shown that savannas can transition to forests in the absence of fire, or conversely that forests can become savannas under the influence of anthropogenic fires (Hoffmann *et al.*, 2012; Veenendaal *et al.*, 2015). Savannas and tropical dry forests can therefore be seen as alternative stable states governed by fire (Veenendaal *et al.*, 2015). Hoffmann *et al.* (2012) propose two types of threshold for the transition between savannas and forests: the fire-resistance threshold characterised by the accumulation of bark that avoids stem death, and the fire-suppression threshold reached when the canopy cover is sufficient to exclude the fire-prone grass layer. Since savanna tree species accumulate bark more quickly than forest species, and forest species form a closed canopy more quickly than savanna species, Hoffmann *et al.* (2012) state that species traits are important in influencing the transition between the two vegetation types. Moreover, the amount of resource available also affects this transition: resource-rich sites can allow both the fire-resistance and the fire-suppression thresholds to be reached more quickly (Hoffmann *et al.*, 2012), explaining why forests generally occur on more fertile soil than savannas (Pennington *et al.*, 2000; Linares-Palomino *et al.*, 2003; Pennington *et al.*, 2006). Fire and soil fertility are therefore the two main interacting abiotic factors affecting the occurrence of forest or savanna in seasonality dry tropical climates (Veenendaal *et al.*, 2015).

Tropical dry forests[5] represent 42% of the extent of the world's tropical forests (Murphy & Lugo, 1986). Miles *et al.* (2006) estimate that they cover a total of more than 1 million km^2 across the three tropical regions, the majority of which is in the Neotropics (66.7%)[6]. Because of their attractive climate for human activities, they have been extensively deforested (Murphy & Lugo, 1986; Maass, 1995) and their current extent covers only a fraction of their original one (Aronson *et al.*, 2005). At the end of the 1980s, Janzen (1988) declared that tropical dry forest was "the most endangered major tropical ecosystem". Unfortunately, tropical dry forest continues to be endangered; Miles *et al.* (2006) estimated that 97% of the current area of tropical dry forest is subject to one or more of the following threats: climate change, forest fragmentation, fire, conversion to agriculture and human population growth. Despite these threats, much less research has been conducted in tropical dry forests compared with moister ones (Sanchez-Azofeifa *et al.*, 2005; Vieira & Scariot, 2006b; Quesada *et al.*, 2009). A good understanding of how their environmental characteristics affect their dynamics is therefore important for their conservation and restoration.

1.5.2 Highly seasonal environment

> "The dry forest may appear uniformly green during the rainy season, but during the dry season this homogeneity changes into a complex mosaic of tens of habitat types distinguished by the different drying rates of different soils and exposures, different ages of succession, and different vegetation types." (Janzen, 1988, p. 131)

The strong seasonality of precipitation is the most characteristic feature of tropical dry forests (Mooney *et al.*, 1995). The alternation of a dry season with virtually no rain, high irradiance and high evaporative demand and a wet season with high precipitation controls the timing of vegetative and reproductive processes (Murphy & Lugo, 1986; Janzen, 1988; Holbrook *et al.*, 1995; Quesada *et al.*, 2009; Maass & Burgos, 2011), leading to striking differences in the forest environment between seasons (Figure 2). In tropical dry forests, the factors limiting plant performance therefore change between seasons from water-limitation during the dry season to light-limitation during the wet season.

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[5] *sensu* Holdridge (1967)

[6] *N.B.* Miles *et al.* (2006) restrict their definition of forest to areas with at least 40% tree cover, which is likely to exclude most savanna and miombo areas.

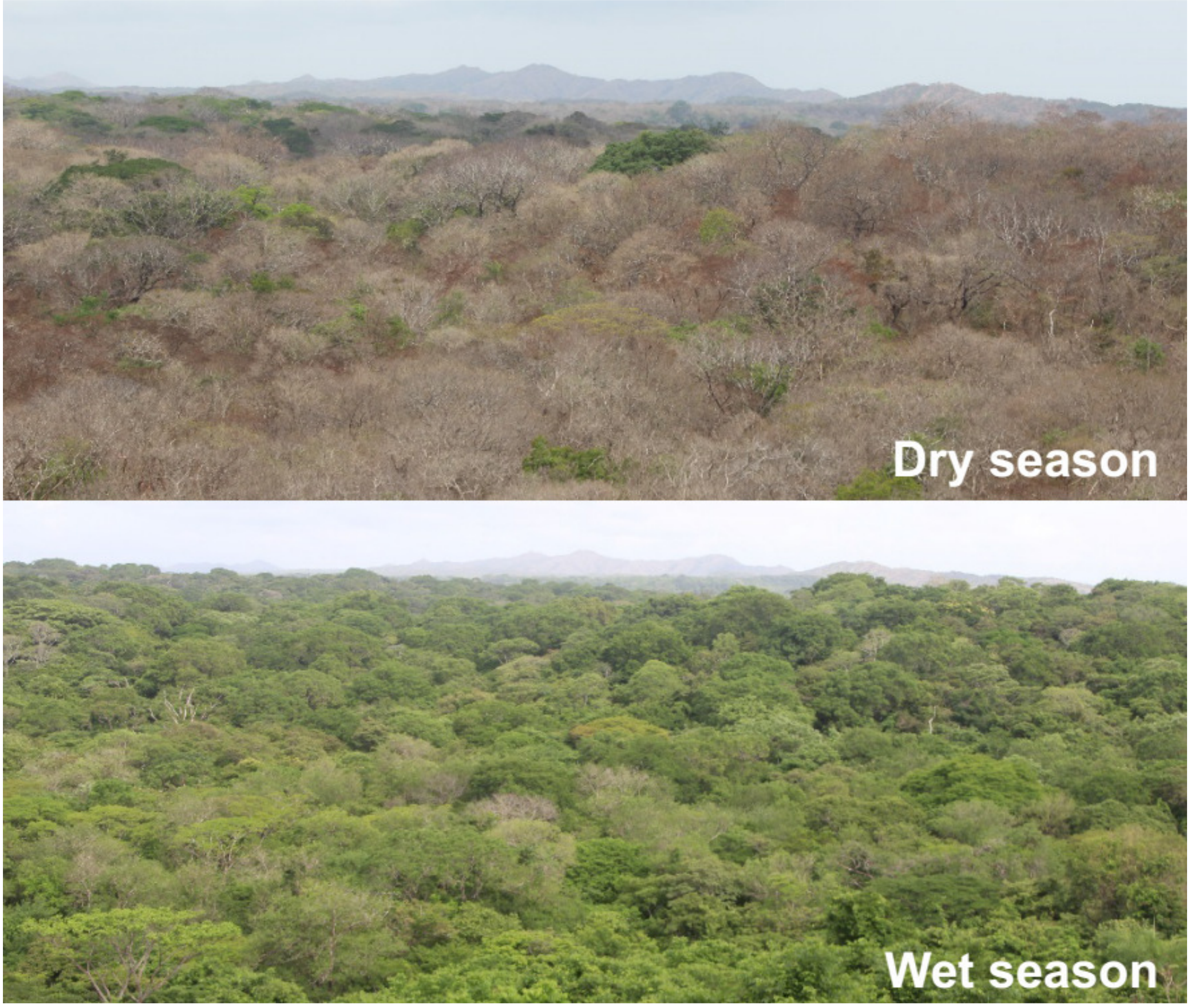

Figure 2. Contrasting green leaf cover between seasons in tropical dry forest. Photos taken from *mirador Tierras Emergidas* (Santa Rosa, Costa Rica) on 10/05/14 (dry season) and 01/07/14 (wet season) (photos Géraldine Derroire).

Most growth of tropical dry forests trees occurs during the wet season (Lopezaraiza-Mikel *et al.*, 2013). The consequence of this limited duration of the growing period is a generally lower net primary productivity than in moister forests (Murphy & Lugo, 1986; Vieira & Scariot, 2006b). Several plant strategies linked to greater tolerance of water limitation during the dry season coexist in tropical dry forests (Giraldo & Holbrook, 2011): woody plants have leaf phenological patterns ranging along a gradient of deciduousness (Frankie *et al.*, 1974; Opler *et al.*, 1980b; Borchert, 1994). The patterns of correlation between leaf phenological habit (*i.e.* evergreen or deciduous character) and other plant functional traits is still insufficiently understood (Hulshof *et al.*, 2013). Some studies show that deciduous trees have leaf trait values associated with the acquisitive end of the leaf economics spectrum (Sobrado, 1991; Pringle *et al.*, 2011), while other studies show a great overlap of functional trait values between deciduous and evergreen trees (Brodribb & Holbrook, 2004; Powers & Tiffin, 2010).

The relationship between rooting depth of trees and their leaf phenology is also variable (Giraldo & Holbrook, 2011). The seasonal changes in canopy openness resulting from tree deciduousness lead to contrasted microclimatic conditions in the understorey (Parker *et al.*, 2005; Lebrija-Trejos *et al.*, 2011).

The seasonality of precipitation also influences reproductive phenology. There is a peak of flowering in each season (Justiniano & Fredericksen, 2000; Frankie *et al.*, 2004) and the timing of flowering depends on resource allocation between vegetative and reproductive processes (Borchert, 1983; Singh & Kushwaha, 2006) and on the pollination agent (Frankie *et al.*, 2004). The timing of fruiting is mainly linked to the dispersal syndrome: seeds dispersed by wind (anemochory) or gravity tend to be produced during the dry season while fleshy-fruited zoochorous species fruit mainly during the rainy season (Ray & Brown, 1994; Sobral Griz & Machado, 2001; Vieira & Scariot, 2006b; Vieira *et al.*, 2008). Most seeds remain dormant until the beginning of the wet season when there is a peak of germination, as found by Garwood (1983) in the seasonal tropical moist forest of Barro Colorado Island. Seedlings emerging early in the wet season can experience a longer growth period before the next dry season, which reduces their mortality (Van Schaik *et al.*, 1993; Khurana & Singh, 2001; Vieira & Scariot, 2006b).

1.5.3 Specificities of regeneration in tropical dry forests

The soil seed bank of tropical dry forests has a low density of accumulated seeds of woody species (Skoglund, 1992; Janzen, 2002). Seeds tend to germinate in the year following their production (Janzen, 2002). Seeds are also lost due to predation, desiccation or fire (Skoglund, 1992; Janzen, 2002; Kennard *et al.*, 2002; Maza-Villalobos *et al.*, 2011b). The soil seed bank therefore has a limited role in the re-establishment of forests through natural processes after another use of the land (Janzen, 2002; Kennard *et al.*, 2002; Lemenih & Teketay, 2005; González-Rivas *et al.*, 2009; Maza-Villalobos *et al.*, 2011b), and secondary succession is generally dependent on other sources of propagules.

Anemochory is a more important mode of seed dispersal in tropical dry forests than in moister ones (Gentry, 1995; Janzen, 2002). Vieira and Scariot (2006b) reported percentages of anemochorous species in several neotropical dry forests ranging from 30% to ~ 60% whereas this percentage was less than 20% in wet and moist forests. Anemochorous species are particularly important for secondary succession because their seeds can travel longer distances in fragmented landscapes and open areas than seeds of zoochorous species (Cubiña & Aide, 2001; Janzen, 2002; Castillo-Nunez *et al.*, 2011). They also tend to be less prone to desiccation than seeds of fleshy fruits (Vieira & Scariot, 2006b), which increases their survival in open areas.

Vegetative reproduction through resprouting is an important mode of regeneration in tropical dry forests (Ewel, 1977; Vieira & Scariot, 2006b). Resprouts can benefit from a more developed root system than seedlings, which allows better acquisition of soil resources, and, in some cases, from reallocation of carbohydrates stored in the roots, which can increase growth and survival rates in the early stage of establishment (Kennard *et al.*, 2002). This mode of regeneration is therefore the one most commonly observed after disturbance events that leave stumps or belowground stem or root tissue, although the importance of vegetative regeneration depends on the precipitation regime and the intensity of disturbance (Sampaio *et al.*, 1993; Kennard *et al.*, 2002; McDonald *et al.*, 2010).

Several authors have suggested that the gap dynamics model, which emphasises the importance of canopy gaps for regeneration in tropical wet forest, may not apply to tropical dry forests (Quesada *et al.*, 2009; Lebrija-Trejos *et al.*, 2010a; Lévesque *et al.*, 2011). Several reasons are proposed for this difference. (1) Because of their more open canopy, light availability may be less limiting for seedling establishment in tropical dry forest, and the shade provided by the canopy may actually improve seed germination and seedling survival rate (Hardwick *et al.*, 1997; Teketay, 1997; Hoffmann, 2000; Cabin *et al.*, 2002a; McLaren & McDonald, 2003a; McLaren & McDonald, 2003b; Vieira *et al.*, 2006; Santiago-Garcia *et al.*, 2008; Wolfe & Van Bloem, 2012). (2) Resprouting is often considered to be a more common regeneration mode in tropical dry forests, as shown by Ewel (1977) who compared wet and dry forest sites in Costa Rica and Puerto Rico, and supported by many study reporting high rates of resprouting in tropical dry forests (as reviewed by Vieira and Scariot, 2006b). Reviewing a number of studies in tropical dry forests, McDonald *et al.* (2010) also showed that resprouting was more common in the drier sites. (3) Tropical dry forests are expected to have a lower rate of canopy gap formation then moister forests. Dickinson *et al.* (2001) found a low occurrence of tree uprooting in tropical dry forests, which they attributed to higher stability of trees due to their shorter stature, higher root-to-shot ratio, lower epiphyte load and lower frequency of storms. However, other evidence from tropical dry forests may actually support the effect of canopy gaps on regeneration. Dechnik-Vazquez *et al.* (2016) found a higher number of individuals and species of seedlings in gaps than under closed canopy, but no difference in species composition. Diamond and Ross (2016) found that the seedlings in canopy gaps generally belonged to late-successional species.

1.5.4 Changes during succession in tropical dry forests

The structure of tropical dry forests changes quickly in the early stages of secondary succession. Based on a quantitative review of 44 studies, Becknell *et al.* (2012) showed a rapid increase in aboveground biomass in the first two decades of succession followed by a slower increase. Similar trends have been found for crown area and basal area (Sovu *et al.*, 2009; Lebrija-Trejos *et al.*, 2010a; Dupuy *et al.*, 2012). The rate of increase of components of forest structure depends on soil characteristics (Powers *et al.*, 2009), distance to old-growth forests (Gomes Reis Lopes *et al.*, 2012) and the intensity of disturbance caused by the previous land use (Molina Colon & Lugo, 2006; Romero-Duque *et al.*, 2007). Becknell *et al.* (2012) showed that aboveground biomass recovered within three to five decades. The amount of biomass depended on the mean annual precipitation of the area, with higher biomass in moister areas, but the time needed to reach it did not. I do not review here the changes in species richness and composition because this is the subject of the meta-analysis presented in paper II and summarized in section 4.2.

These structural changes have obvious consequences for the forest microclimate, yet they are rarely quantified. The only study of which I am aware is that of Lebrija-Trejos *et al.* (2011), who studied a 60-year chronosequence in Mexico. They found that understorey light levels and air and soil temperatures decreased while relative humidity increased, during succession. Soil water availability showed an initial increase followed by a decrease, probably as a result of increased transpiration of canopy trees. More studies on the changes in environmental conditions during succession are needed.

In comparison with moister tropical forests, aboveground biomass generally accumulates at a lower absolute rate in tropical dry forests (Ewel, 1977; Poorter *et al.*, 2016). However, because the quantity of biomass and basal area in old-growth forests is also lower in drier forests (Murphy & Lugo, 1986; Poorter *et al.*, 2016), the time needed to recover the structure of an old-growth forest in tropical dry forest can be similar to that in moister forests (Quesada *et al.*, 2009; Poorter *et al.*, 2016).

Because of their generally lower structural complexity, the difference in understorey light levels between the early and later stages of succession is smaller in tropical dry forests than in moister forests, and the changes in temperature and humidity may be stronger drivers of change in plant communities during succession (Lebrija-Trejos *et al.*, 2010b; Lebrija-Trejos *et al.*, 2011). As a result, the change in plant strategies during succession is expected to differ between tropical dry and moister forests (Lohbeck *et al.*, 2013; Letcher *et al.*, 2015). In tropical wet forests, the decrease in understorey light availability with succession leads to a change from acquisitive to conservative strategies (Boukili, 2013; Lohbeck *et al.*, 2013; Lohbeck *et al.*, 2015). However in tropical dry forests, the high drought tolerance generally associated with conservative strategies (Reich, 2014) can reduce mortality in the face of high evaporative demand in early successional environments, which suggests a change from conservative to acquisitive strategies with succession. This hypothesis has only received mixed support from field studies (Lebrija-Trejos *et al.*, 2010b; Lohbeck *et al.*, 2013; Becknell & Powers, 2014; Buzzard *et al.*, 2015), and leaf phenological habit and morphological traits that contribute to leaf cooling and control of water status can be more important in explaining changes in community functional composition during succession than those traits generally associated with leaf economics strategies (Lebrija-Trejos *et al.*, 2010b; Lohbeck *et al.*, 2015).

1.6 Ecological restoration in tropical forests

Ecological restoration, "assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed" (SER, 2016), can increase biodiversity and the delivery of ecosystem services (Chazdon, 2008; Holl, 2012). Ecological restoration requires a good understanding of ecological processes (Hardwick *et al.*, 2004; Aronson & Vallejo, 2008; Holl & Aide, 2011), among which succession is of the utmost importance (Palmer *et al.*, 1997; Young, 2000; Hobbs *et al.*, 2007). Indeed, most restoration projects aim to mimic and accelerate this natural process (Dobson *et al.*, 1997; Palmer *et al.*, 1997; Walker *et al.*, 2007), maximizing efficiency and minimizing human input, and therefore minimizing the cost of restoration projects (Hardwick *et al.*, 2004; Chazdon, 2008). In this section, I do not aim to review exhaustively the techniques of ecological restoration of tropical forests but rather to present an overview of the most common ones and to show how ecological restoration can benefit from knowledge acquired by the study of natural succession.

There are a range of restoration techniques requiring different levels of input from the practitioner (Chazdon, 2008; Griscom & Ashton, 2011). Passive restoration, also called "unassisted restoration", requires no human intervention besides the removal of activities causing degradation (*e.g.* human-induced fire, grazing) (Holl & Aide, 2011; Zahawi *et al.*, 2014). Such a technique is effective, and sometimes better than more active intervention, in cases where there is no major barrier to the arrival and successful establishment of forest tree species (Sampaio *et al.*, 2007; Holl, 2012). In other cases, a variety of active restoration techniques can be used to alleviate these barriers: for example, perches placed in the restoration site can attract birds and hence increase seed inputs (Shiels & Walker, 2003; Graham & Page, 2012), and removing grass can reduce competition and favour seedling establishment (Hardwick *et al.*, 1997; Cabin *et al.*, 2002a). These techniques are often referred to as "assisted natural regeneration" or "accelerating natural regeneration" (Hardwick *et al.*, 1997; Shono *et al.*, 2007). The introduction of woody species' individuals, as seed in the case of direct seeding or as planted seedlings, is necessary when the arrival of propagules is low or absent, but can also be used to accelerate succession or to introduce desired species that are missing (Griscom & Ashton, 2011). Observational and experimental studies carried out in natural forests can improve our understanding of the mechanisms and factors influencing degradation and succession (Figure 1) and provide insight into site-specific opportunities as well as constraints to restoration in order to select the most appropriate and cost-effective technique (Chazdon, 2008; Holl & Aide, 2011).

There are two main restoration techniques based on the plantation approach. Planting evenly-spaced seedlings across the whole site, in monoculture or mixed stands, is the classical method (Lugo, 1997; Parrotta *et al.*, 1997). The more recent applied-nucleation technique is gaining momentum as it offers a reduced-cost alternative. It is based on planting small patches of trees that then act as regeneration nuclei. With time, these nuclei expand and eventually coalesce, forming a continuous and heterogeneous tree cover (Holl *et al.*, 2010; Reis *et al.*, 2010; Corbin & Holl, 2012; Zahawi *et al.*, 2013). Applied nucleation and other restoration planting methods aiming to foster the establishment of other species besides the planted ones are based on application of the nurse plant effect (described in section 1.3.2): planted trees improve seed deposition, reduce grass competition and provide suitable microclimatic conditions for the arrival and establishment of other woody plants (Parrotta *et al.*, 1997; Hardwick *et al.*, 2004; Griscom & Ashton, 2011; Holl, 2012). These techniques therefore rely on the availability of propagules dispersed from the surroundings of the restoration site (Florentine & Westbrooke, 2004; Holl, 2012). The choice of species used for restoration planting and applied nucleation is, however, important because this choice influences the subsequent generations of trees that establish and therefore the long-term outcome of restoration (Parrotta, 1995; Murcia, 1997; Padilla & Pugnaire, 2006). In some cases, there is a risk of competition between planted trees and newly establishing ones that can slow down succession (Padilla & Pugnaire, 2006; Sampaio *et al.*, 2007).

Although planting a monoculture of exotic species has been used for restoration (Lugo, 1997; Feyera *et al.*, 2002), the use of a mixture of native species is increasingly preferred (Chazdon, 2003; Griscom & Ashton, 2011; Holl, 2012). This technique requires a good knowledge of the ecology of these species for which the study of forest undergoing natural succession can be valuable. The “framework species” method aims to identify a set of suitable species for restoration planting based on their establishment success in open areas and capacity to quickly form a canopy, attract animal dispersers and provide suitable microclimatic conditions for the establishment of other species (Elliott *et al.*, 2003; Holtz & Placci, 2005). A functional trait-based approach can be useful to narrow down the list of candidate species by helping predict their performance and informing on other desired characteristics to meet restoration objectives (Martínez-Garza *et al.*, 2005; Martinez-Garza *et al.*, 2013; Ostertag *et al.*, 2015). Intraspecific variation of traits can also be useful to assess the potential plasticity of a species in response to a variety of environmental conditions (Martínez-Garza *et al.*, 2005).

2 Objectives

The overall objective of my research is to contribute field-based knowledge to advance ecological theories of secondary succession in tropical dry forests. I especially focus on (1) the models and long-term trajectories of succession and their drivers (papers II and IV) and (2) the underlying mechanisms and processes (papers I, III and study of seed fate). Each study considers a subset of the overall framework (Figure 1) by focussing on a restricted spatial and temporal scale (Figures 3 to 7). By providing information on the opportunities and barriers to natural succession, my results can have applications for science-based ecological restoration practices. The specific objectives are the following:

Identify the mechanisms by which established trees influence the establishment of woody plants leading to later stages of succession

Paper I focuses on the community and individual scales. It aims to identify the mechanisms of positive and negative plant-plant interactions between adult trees and each stage of the regeneration of young woody plants during secondary succession (Figure 3). The methodological approach of this study is the systematic review of observational and experimental studies. Understanding of these mechanisms has application for the use of the nurse plant effect in ecological restoration.

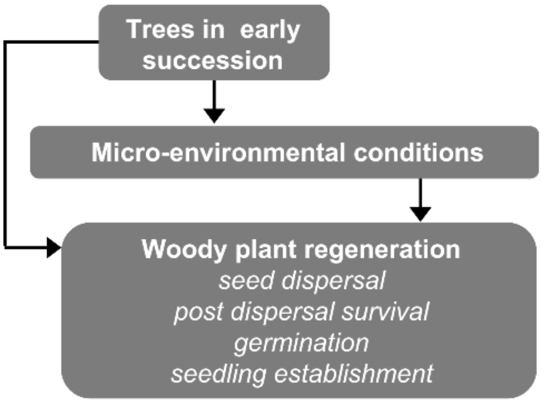

Figure 3. Conceptual framework of paper I.

Assess the resilience capacity of tropical dry forest tree and shrub communities and identify the factors affecting their degree of resilience

Paper II considers the long-term trajectories of succession. It uses a meta-analysis approach to assess the resilience capacity of taxonomic diversity and composition of tree and shrub communities in successional tropical dry forests (Figure 4). It also tests if regional abiotic environmental factors (precipitation regime and water availability) and land use history of the site influence the rate and directionality of changes in taxonomic diversity and composition. The results can help to identify the opportunities and barriers to restoration of the diversity of tropical dry forests and guide the choice of restoration strategies (passive *versus* active restoration).

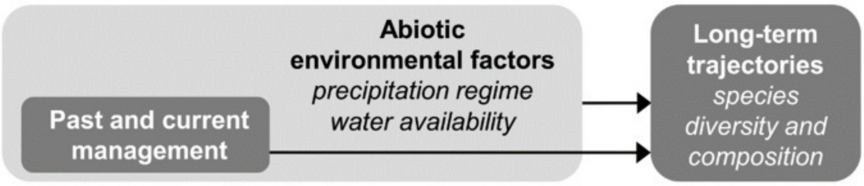

Figure 4. Conceptual framework of paper II.

Identify the factors structuring woody plant assemblages under isolated pasture trees

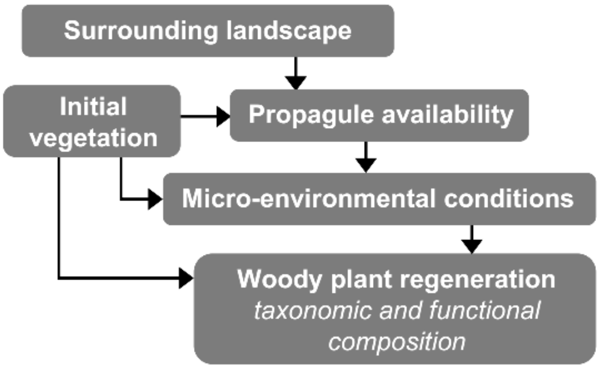

Figure 5. Conceptual framework of paper III.

Paper III considers the first stage of secondary succession in pasture sites. The aim is to test the importance of landscape factors and attributes of isolated trees in explaining the properties of the woody plant regeneration assemblages beneath their crowns (Figure 5). Both the taxonomic and functional compositions of the regeneration assemblage are considered. The methodological approach is survey of the woody vegetation regenerating under a large sample of pasture trees. The results can inform practitioners about the factors to consider when selecting species to plant to initiate restoration (or which trees to prioritise for protection within pasture), especially when using the technique of applied nucleation.

Identify the direction and drivers of change in functional composition of sapling communities during succession

Paper IV considers the long-term trajectories of succession at the scale of the tree community. It uses a functional trait-based approach and assesses the relative contribution of species turnover and intraspecific variation to the response of community-level trait values to changes in environmental conditions (Figure 6). The methodological approach is measurement of leaf functional traits of all saplings in plots of two chronosequences. The results of this study can inform on the values of functional traits associated with different stages of succession.

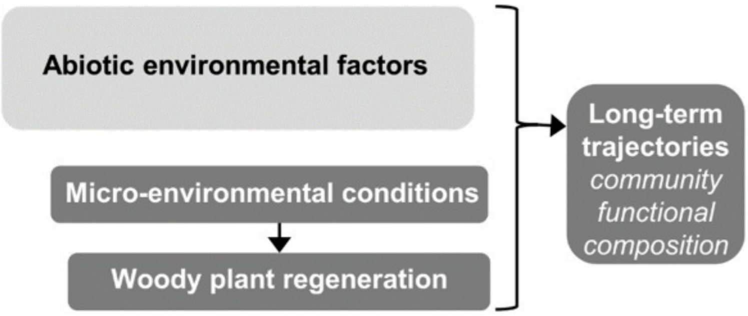

Figure 6. Conceptual framework of paper IV.

Assess the influence of the changing abiotic and biotic environmental conditions during secondary succession on the fate of tree seeds and identify the underlying mechanisms

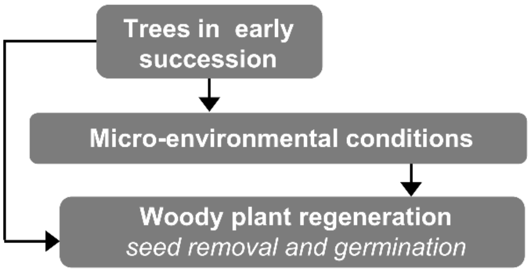

Figure 7. Conceptual framework of the study of seed fate.

The study of seed fate addresses one of the research gaps identified by Paper I. It focuses on the community and individual scales and considers an open pasture area, and young and intermediate-aged secondary forests. It uses an experimental approach to test the relative influence of shading by tree canopies and leaf litter as factors determining the fate of seeds (removal by predators and germination) artificially dispersed into the sites (Figure 7). The results will provide information on the potential of restoration by direct sowing.

3 Material and methods

3.1 Study area and study sites

Three of the studies (papers III and IV and the study of seed fate) were based on field data that I collected in, or in the surroundings of, the *Área de Conservación de Guanacaste* (ACG) (ACG, 2016), in the north-west of Costa Rica (Figure 8). This area has been extensively used for agriculture (mainly cattle farming, and sugar cane and cotton cultivation) and wood extraction since the Spanish conquest in the early 1500s, which led to the clearing of most of the forested area by the 1970s. This trend started to reverse in the 1980s as a result of the combination of conservation policies and changes in economic activities (Calvo-Alvarado *et al.*, 2009). In the mid-1980s, an ambitious restoration project started at the instigation of Dr Daniel Janzen (Janzen, 2002; Aronson *et al.*, 2005). This project is mainly based on fostering the natural re-establishment of the forest by alleviating the main barriers to forest regeneration through the purchase of degraded agricultural land, the exclusion of cattle and the control of anthropogenic fires (Janzen, 2002). Originally centred around the 10 000 ha of tropical dry forests of the Santa Rosa National Park, the conservation area has gradually extended to reach the current 163 000 ha of protected area comprising marine, tropical dry forest, cloud forest and rain forest habitats (ACG, 2016).

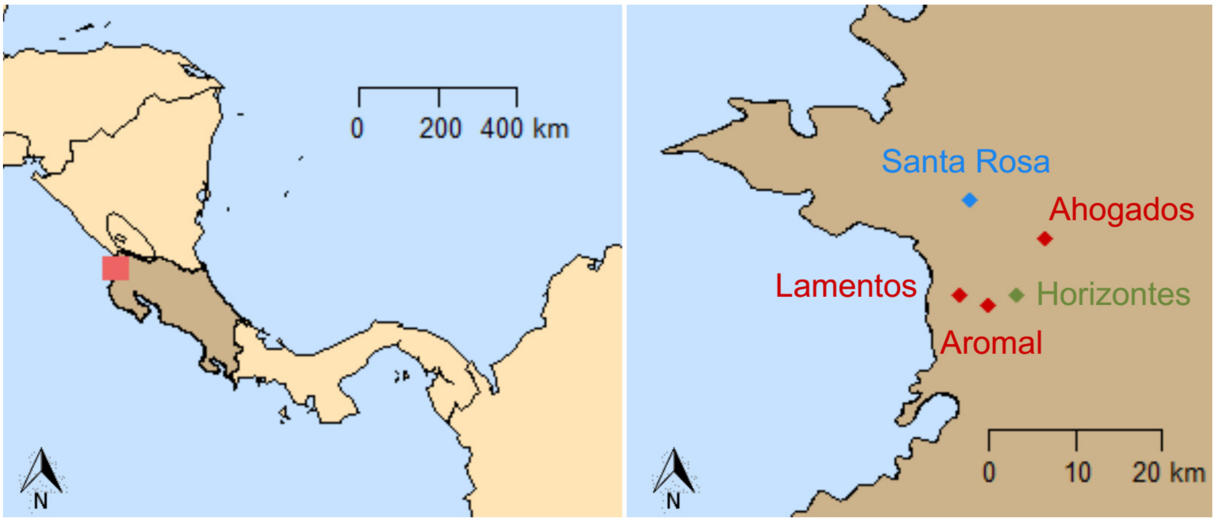

Figure 8. Study area and study sites. The red square on the map on the left indicates the area enlarged on the right. The map on the right shows the study sites: red for paper III, blue for paper IV and green for the study of seed fate.

The study area is at the wet end of the rainfall gradient of tropical dry forests, with ~ 1640 mm mean annual precipitation (data from the meteorological station of Liberia 10.58°N; 85.53°W collected between 1958 and 2014, Instituto Meteorológico Nacional de Costa Rica, 2016). The climate is characterised by strong seasonality of precipitation with a 5-6 month dry season and more than 95% of the mean annual precipitation falling during the May-November wet season (Figure 9). Mean temperatures vary little over the year and have an annual mean of 27.5 °C (data from the meteorological station of Liberia collected between 1977 and 2014, Instituto Meteorológico Nacional de Costa Rica, 2016). Maximum temperatures can exceed 40 °C (personal measurement).

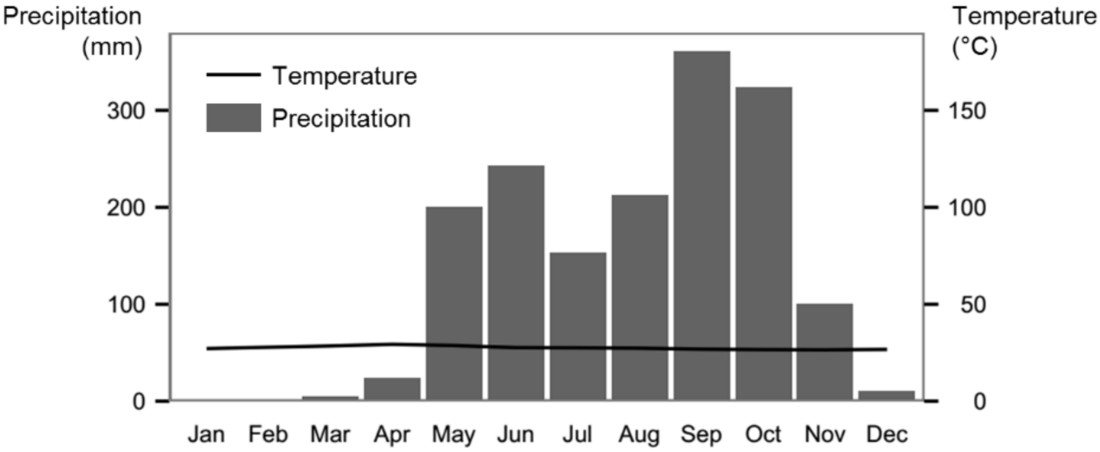

Figure 9. Climate diagram of the study area. Data *Instituto Meteorológico Nacional de Costa Rica*, meteorological station of Liberia 10.58°N; 85.53°W. Precipitation 1958-2014, temperature 1977-2014 (Instituto Meteorológico Nacional de Costa Rica, 2016).

The landscape is a mosaic of pastures and secondary forests of different ages, resulting from the history of land use. The natural vegetation is tropical dry forest (Holdridge *et al.*, 1971) formed by a mixture of evergreen trees and trees of diverse degrees of deciduousness (Borchert *et al.*, 2004). Janzen (2002) estimated that an old-growth forest in the area has 30-60% of its canopy space occupied by evergreen trees, while the proportion is higher in the understory. Woody lianas are abundant in successional forests but less so in the closed-canopy old-growth forests (Sanchez-Azofeifa *et al.*, 2009). In nearby tropical dry forest, Frankie *et al.* (1974) found that 30% of the species were anemochorous, which is a relatively low proportion when compared with other tropical dry forests (Vieira & Scariot, 2006b), and 50% of species had fleshy fruits.

The dry forests of Guanacaste host a high number of plant species. Janzen and Liesner (1980) listed almost 1000 species of plants, excluding grasses and non-vascular cryptogams, encountered in Guanacaste. Gillespie *et al.* (2000) found an average of 12 species of trees and shrubs and 4.5 species of lianas per 100 m^2 in Santa Rosa, making this the richest of the seven tropical dry forest sites that they studied in Nicaragua and Costa Rica, and one of the richest ones in the whole Neotropics. As in all Neotropical dry forests with the exception of the Caribbean and Florida, Leguminosae is the most species-rich family in Guanacaste (Gentry, 1995; Gillespie *et al.*, 2000; Pennington *et al.*, 2006; Pennington *et al.*, 2009). Bignoniaceae is the family represented by the most species of lianas (Gentry, 1995; Gillespie *et al.*, 2000). There is generally little overlap in species composition between these dry forests and the neighbouring moist forests (Murphy & Lugo, 1995). This floristic differentiation between tropical dry and wet forests is consistent with the finding of Dexter *et al.* (2015) that, within the Neotropics as in the other tropical areas, there is a clustering of floristic composition by vegetation type[7]. This trend indicates strong phylogenetic biome and niche conservatism, only lineages with adaptations enabling survival of drought being able to establish in tropical dry forests (Hughes *et al.*, 2013). However, Gentry (1995) reported the occurrence of moist forests plants, such as species in the genera *Ficus* and *Psychotria*, in the tropical dry forests of Guanacaste, which he attributed to the presence of moister gallery forests in the dry forest landscape. At the continental scale, the tropical dry forests of Costa Rica have floristic affinities with a wide range of tropical dry forests including those in Mexico and Central America, the Caribbean and the Northern part of South America (Colombia and Venezuela), with different classifications showing stronger affinities with one or the other of these floras (Linares-Palomino *et al.*, 2003; Linares-Palomino *et al.*, 2011). The affinities of floristic

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[7] *N.B.* At the global scale, however, the clustering by continent is stronger.

composition between these areas results from the dispersal opportunities provided by the land bridge of the Panama Isthmus since its closure ~3 million years ago, but also through island stepping stones before that (Murphy & Lugo, 1995; Linares-Palomino *et al.*, 2003; Bagley & Johnson, 2014).

Natural fires are extremely rare in Guanacaste (Hartshom, 1983). No fires caused by lightning have been observed during the dry season and natural fires are limited to those caused by volcanic activity (Janzen, 2002). As a consequence, there are no natural savannas in Guanacaste, and there is no evidence for the presence of savannas in the past (Janzen, 2002). On the other hand, anthropogenic fires are frequent and fostered by the presence of fire-prone exotic grasses such as *Hyparrhenia rufa* in pasture sites (Daubenmire, 1972; Janzen, 2002). They are a major barrier to forest regeneration in the early stage of succession and their control is therefore a key factor in the success of the restoration of the dry forest in Guanacaste (Janzen, 2002).

For paper III, I worked in three active pasture sites located in private land (Ahogados 10.80°N, 85.54°W, Lamentos 10.74°N, 85.63°W and Aromal 10.73°N, 85.60°W). For paper IV, I collected data in Santa Rosa (10.84°N, 85.62°W), in plots in successional forests located to span two chronosequences in each of two distinct forest types (oak dominated forests and forests with a more even mixture of species). For the study of seed fate, I worked in an open area and two successional forests in the Experimental Forest Station of Horizontes (10.74°N, 85.57°W) (Figure 8).

3.2 Data acquisition

3.2.1 Systematic review of the literature

For papers I and II, I used data and observations from previously published studies. To increase objectivity, comprehensiveness and repeatability, I followed a systematic protocol to search for and select studies (Pullin & Stewart, 2006; Woodcock *et al.*, 2014). I searched at least two databases of scientific literature using an explicit search string. I then selected the studies following clearly reported inclusion criteria.

3.2.2 Observational approach: vegetation survey

Papers II, III and IV use an observational approach based on vegetation surveys to study changes occurring during succession at the scale of whole tree communities.

Paper II: species diversity and composition

For paper II, I used raw data provided by the authors of the included studies in the form of floristic tables of species abundance for plots at different successional ages. The tree community of each plot was characterised in terms of species richness, species evenness and similarity of species composition with the composition of old-growth forests.

To calculate species richness, I used the standardisation method proposed by Colwell *et al.* (2012) to account for differences in stem density among plots. I used the individual-based approach, as I had one sample for each community (*i.e.* plot), with multinomial model to be able to standardise the species richness to a chosen number of individuals (15 in this case). When the actual number of individuals in the plot was greater than 15, the species richness was obtained by rarefaction (interpolation) and when it was less than 15, the species richness was obtained by extrapolation. Combining the two methods was not a problem because the interpolation and extrapolation curves joined smoothly (Colwell et al. 2012). I chose to standardise the richness to a number of 15 individuals because 15 was less than three times the actual number of individuals in 98.5% of the plots; Colwell et al. (2012) specifically warn against extrapolating to a number of individuals that is more than three times the actual number. I used the function *iNEXT* of the package *iNEXT* (Hsieh *et al.*, 2015) in R (R core team, 2015) to calculate species richness.

To calculate species evenness, I used two of the most common evenness indices, Shannon and Simpson (Magurran, 2005). Both are based on a corresponding measures of species diversity, the Shannon and Simpson diversity indices, respectively (Maurer & McGill, 2011) and differ is their approach and properties (Smith & Wilson, 1996; Magurran, 2005; Jost, 2010). They notably differ in their dependency on species richness, the Shannon index being dependent while the Simpson index is not (Jost, 2010). Both indices were calculated using the function *diversity* in the package *vegan* (Oksanen *et al.*, 2015) in R.

To calculate the similarity of species composition in each successional plot with the composition of old-growth forests, I calculated two similarity indices, the Sørensen and Chao-Sørensen indices, for each pair of successional and old-growth forest plots of each study (Chao *et al.*, 2005). When a study considered several old-growth plots, I averaged the similarity across old-growth forest plots for each successional plot. The Sørensen index is an occurrence-based index: it compares the number of shared species to the mean number of species in a single plot (Jost *et al.*, 2011). For this reason, it gives a more local perspective than the Jaccard index, which compares the number of shared species to the number of species in the combined two plots. I calculated the Sørensen index using the function *betadiver* in the package *vegan* (Oksanen *et al.*, 2015) in R. The Chao-Sørensen index is an abundance-based index: it assesses the probability that two randomly chosen individuals (one in each plot considered) belong to one of the species shared between the two plots. I calculated this index using my own function in R.

I had two reasons for considering two indices. (1) While the occurrence-based Sørensen index allowed me to assess the recovery of a list of species during succession, the abundance-based Chao-Sørensen index allowed me to assess the recovery of the hierarchy of species (*i.e.* their relative abundance). The two indices give different information that can be applied respectively to restoration activities with different objectives. (2) Because the Chao-Sørensen index assesses the probability that two randomly chosen individuals belong to a shared species, if the shared species are abundant (or rare) in one or both plots, their probability to be randomly chosen will be higher (or respectively lower) so the index is expected to be higher (or respectively lower). On the other hand, the occurrence-based Sørensen index will not change. I therefore considered that the Chao-Sørensen index gives more weight to the common species. I acknowledge that another solution to study the difference in the recovery of common and rare species could have been to use the Horn and the Morisita-Horn indices, two abundance-based similarity indices giving more weight to the rare and common species, respectively (Jost *et al.*, 2011). I have chosen not to use the Bray-Curtis index, which is another commonly used abundance-based index of similarity, because it is very sensitive to large differences in the number of individuals between the plots considered (Jost *et al.*, 2011), which was likely to happen with the successional data that I studied.

Paper III: species and functional compositions

For paper III, I surveyed the woody vegetation regenerating under the crown of 90 isolated trees in pasture. I characterised these regeneration assemblages in terms of the number of individuals, number of species and functional composition. For the functional composition, I considered categorical functional traits (life form, dispersal syndrome[8], leaf phenological habit, leaf compoundness and membership of the Leguminosae family) based on literature and on-line resources. I also characterized the isolated trees by their position in the landscape relative to nearby tree patches (in terms of distance and area of tree patches in buffers ranging from 100 to 1000 m around the focal isolated tree), using orthophotos analysed in ArcGIS. I

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[8] For seed dispersal type, I considered two categories (zoochorous *versus* anemochorous and autochorous). For zoochorous species, the data available did not allow me to distinguish accurately between the different types of animal dispersers.

also considered structural variables (*e.g.* height, crown area) and functional traits (seed dispersal type, leaf phenological habit and ability to fix nitrogen) of the isolated trees.

Paper IV: community functional composition

For paper IV, I surveyed all saplings present in 12 plots (5 x 50 m) located in forest of different successional ages. For each sapling, I measured the following leaf functional traits using standard protocols (Cornelissen *et al.*, 2003; Perez-Harguindeguy *et al.*, 2013):

- traits associated with resource economics strategies: specific leaf area (SLA), leaf density, leaf area (LA), leaf dry matter content (LDMC), petiole length, leaf thickness, and leaf nitrogen (LNC), phosphorous (LPC) and carbon concentration (LCC),
- traits associated with dry and hot conditions: leaf compoundness, leaf pubescence, leaf phenological habit, leaf density and LDMC,
- stoichiometric ratios: C/N and N/P,
- membership of the Leguminosae family.

I then calculated two types of trait community mean values: (a) the specific mean using a trait value *per species* and *per plot* and therefore taking into account intraspecific variation of trait values and (b) the fixed mean using a mean trait value *per species* calculated *across plots* and therefore ignoring intraspecific variation (Lepš *et al.*, 2011).

3.2.3 Experimental approach

For the study of seed fate, I used an experimental approach to test the influence of tree cover in secondary forest on the fate of seeds dispersed underneath. I used a fully factorial design with four factors (four replicates for each combination of factors and 20 seeds per replicate) (Figure 10):

- site: two forest sites of different successional ages (14 and 30 years old) and an open area,
- litter treatment: naturally accumulating litter and litter removal,
- predation treatment: with or without wire mesh protection against predation (holes in mesh are 1.27 x 1.27 cm),
- seven species of seeds.

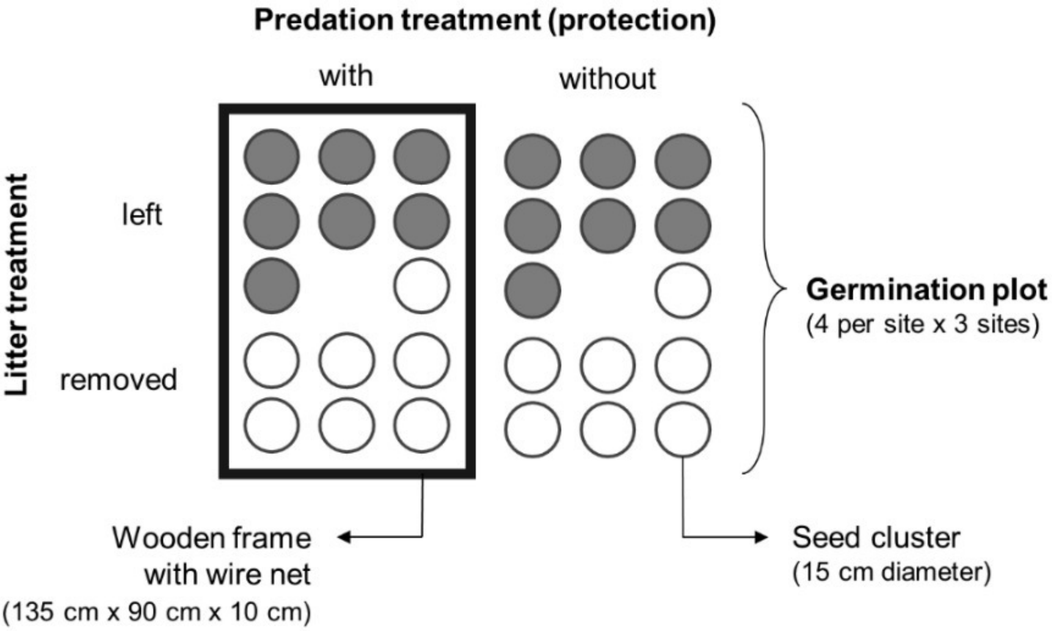

Figure 10. Experimental design for the study of seed fate. Each seed cluster contains 20 seeds of a given species. All depots of a same germination plot have a different combination of species, litter and predation treatments.

I tested seven species that are common in the tropical dry forests of Guanacaste, have contrasting seed traits (seed dispersal type, size and shape) and belong to different families (though two species of the common Leguminosae family were tested) (Figure 11).

Figure 11. Seeds of the seven species tested in the study of seed fate. The approximate length of *Simarouba amara* seeds is 2 cm. Photos Géraldine Derroire.

For each seed cluster, I monitored, every two weeks over 12 weeks, the proportion of seeds having one of the following fates:

- germination,
- removal (seed no longer present in the cluster),
- pathogen attack or predation *in situ*.

3.2.4 Environmental conditions

For paper II, I considered several environmental factors at the regional and site scales for each reviewed study. I tested their influence on the direction and rate of change in species diversity and composition during succession. These factors were:

- the former land use of the site before the forest started to re-establish,
- the precipitation regime (mean annual precipitation and number of dry months),
- the availability of water (measured as the ratio between annual potential evapotranspiration and mean annual precipitation).

For paper IV and the study of seed fate, I measured a set of microclimatic factors expected to change during succession (those followed by an asterisk were considered only for the study of seed fate): air temperature (logged over several days), soil temperature* (repeated measurements at different times), canopy openness (measured using hemispherical photographs), red/far red light ratio* (repeated measurements at different times), air humidity (repeated measurements at different times) and soil moisture (repeated measurements at different times. For paper IV the measurements were taken by Bonnie Waring). For paper IV, I also considered soil physical and chemical factors (data collected by Powers *et al.*, 2009) that I assumed were not influenced by changes occurring during succession, to assess possible bias (caused by indirect relationships between the variables of interest due to their correlation with site environment), which is an inherent risk of the chronosequence approach.

3.3 Data analysis

3.3.1 Meta-analysis

For the meta-analysis conducted in paper II, I used statistical methods adapted to summarize the results of several studies. Meta-analyses allow the calculation of an overall effect size (in my study, rates of change in species diversity and composition indices). They combine the effect sizes calculated for each study while accounting for their unequal precision, by weighting them by their variance (Koricheva & Gurevitch, 2013). To explain the heterogeneity between studies, I then carried out meta-regressions, a type of meta-analysis enabling to test the effect of covariates (also called moderators, in my study the duration of succession studied, the previous land use, the rainfall regime and water availability) on the magnitude of effect size to be tested (Mengersen *et al.*, 2013). All analyses were performed using the package *Metafor* (Viechtbauer, 2010) in R.

For paper I, it was impossible to conduct a meta-analysis because of the low number of studies meeting the inclusion criteria, the heterogeneity of their methodological approaches and the absence of reporting of the variance of the results in most cases.

3.3.2 Ordination

I used ordination methods for the variables that were multivariate (taxonomic composition for paper III and functional trait association for paper IV).

For paper III, I tested the effect of the attributes of isolated trees on the taxonomic composition of the regeneration assemblages using redundancy analysis (RDA). This is a canonical ordination technique that combines regression and principal component analysis (PCA) (Borcard *et al.*, 2011). It computes axes that best explain the variation of the response variable and expresses each axis as a linear combination of the explanatory variables (Legendre & Gallagher, 2001). I carried out a forward model selection procedure to identify the model with the best sets of explanatory variables (Borcard *et al.*, 2011).

For paper IV, I used the RLQ method to understand the relationship between environmental factors and functional traits. In this analysis, functional traits were considered together (a multi-trait approach) to understand plant strategies and trade-offs. RLQ is an ordination technique analysing the matrices of species distribution across plots, environmental factors of plots and species/individuals traits to find axes that maximize the squared cross-variance of linear combinations of environmental factors and traits (Dray *et al.*, 2014). The resulting coefficients were then presented graphically. I used two partial RLQs (Wesuls *et al.*, 2012), performed with the package *Ade4* (Dray & Dufour, 2007) in R, to separate the part of the trait-environment relationship that was due to intraspecific variation of trait values from these due to species turnover.

3.3.3 Regression

I used regression models (linear model, generalised linear models (GLM) or mixed-effects models, depending on the distribution of the response variable and the necessity to include a random factor), to test:

- the effect of the precipitation regime on the importance of positive and negative effects of established trees on regeneration (paper I),
- the influence of landscape factors and attributes of isolated trees on properties of the regeneration assemblage under their crowns (paper III),
- the effect of experimental treatments on the proportion of seed showing each recorded fate (study of seed fate),
- the changes in trait values with ontogeny and the effect of environmental factors on community weighted mean values for each functional trait separately (single-trait approach) (paper IV). I expressed the sum of squares obtained by linear regression of each community value with one or the other of the two types of community weighted means presented in section 3.2.1 as a percentage of the total sum of squares to get the contribution of species turnover and intraspecific variation to the response of communities to environmental factors, following the method of Lepš *et al.* (2011) and using the function *trait.flex.anova* that they coded for R (Lepš *et al.*, 2011).

Table 1 presents a summary of the methods used for each study.

Table 1. *Overview of methods.*

Study	Study sites	Methodological approach		Data analysis
Paper I	Tropical dry forests across the world	Review	-	Narrative review, regression
Paper II	Tropical dry forests across the world	Review	Taxonomic	Meta-analysis
Paper III	Pasture sites (Ahogados, Aromal, Lamentos; Costa Rica)	Observational	Taxonomic and trait-based	Ordination, regression
Paper IV	Successional forests (Santa Rosa; Costa Rica)	Observational	Trait-based	Ordination, regression
Study of seed fate	Open site and successional forests (Horizontes; Costa Rica)	Experimental	Taxonomic	Regression

4 Main results and specific discussion

4.1 Effects of established trees on woody regeneration

This section presents and discusses the main results of paper I.

4.1.1 Positive *versus* negative interactions at each stage of regeneration

The reviewed studies showed the importance of the effects of trees establishing in the early stages of secondary succession on the subsequent regeneration of woody species. Observational studies provided support for potential net effects while experimental studies enabled understanding of the mechanisms underlying these effects. I discuss below the type of effect (positive or negative) and the possible underlying mechanisms for each stage of the process of regeneration: seed dispersal, survival of seeds, germination and seedling establishment, and I summarize them in Figure 12.

Effects on seed dispersal

The five studies researching the effects of established trees on seed dispersal showed an overall positive effect of the presence of trees. This effect is mediated by animal dispersers that are attracted by established trees (Vieira & Scariot, 2006b), resulting in a higher proportion of zoochorous species under tree canopies (Wydhayagarn *et al.*, 2009) and an increase in this proportion with succession (Opler *et al.*, 1980a).

Effects on post-dispersal survival of seeds

The three studies researching the effects of established trees on post-dispersal seed survival suggested that there can be both a positive direct effect, the canopy cover mitigating the conditions responsible for seed desiccation (Vieira & Scariot, 2006a), and an indirect effect mediated by seed predators. For the latter, there was evidence of both a decrease (Hammond, 1995) and an increase (Wassie *et al.*, 2010) in seed predation and removal under closed canopies. Overall, the effect on post-dispersal seed survival is complex as it depends on the type of seed, the type of consumer and the successional stage. More studies, especially experiments, are needed to get a better understanding of these effects.

Effects on seed germination

Hardwick *et al.* (1997) found a higher germination rate under forest cover than in open areas, supporting a positive effect of established trees on seed germination. Experimental studies manipulating shading and watering suggest that this effect occurs via increased moisture conditions under tree cover (Hardwick *et al.*, 1997; McLaren and McDonald, 2003a; but compare Ray and Brown, 1995). However, the response of seed germination was species-specific (Hardwick *et al.*, 1997) and further studies are needed to identify the seed traits explaining the difference in species' responses.

Effects on seedling establishment

The reviewed studies suggested a positive effect of established trees on seedling survival, mediated by mitigation of desiccating conditions during the dry season, and an overall negative effect on seedling growth through limitation of light during the wet season (Cabin *et al.*, 2002a; McLaren & McDonald, 2003b; Wolfe & Van Bloem, 2012). However, the effects on seedling growth are complex: they depend on the successional stage (Hammond, 1995), the leaf phenology of both the established trees (Gerhardt, 1996) and the seedlings (Ray & Brown, 1995) and can be altered by changes in resource allocation by the seedlings in response to environmental variation (Rincón & Huante, 1993).

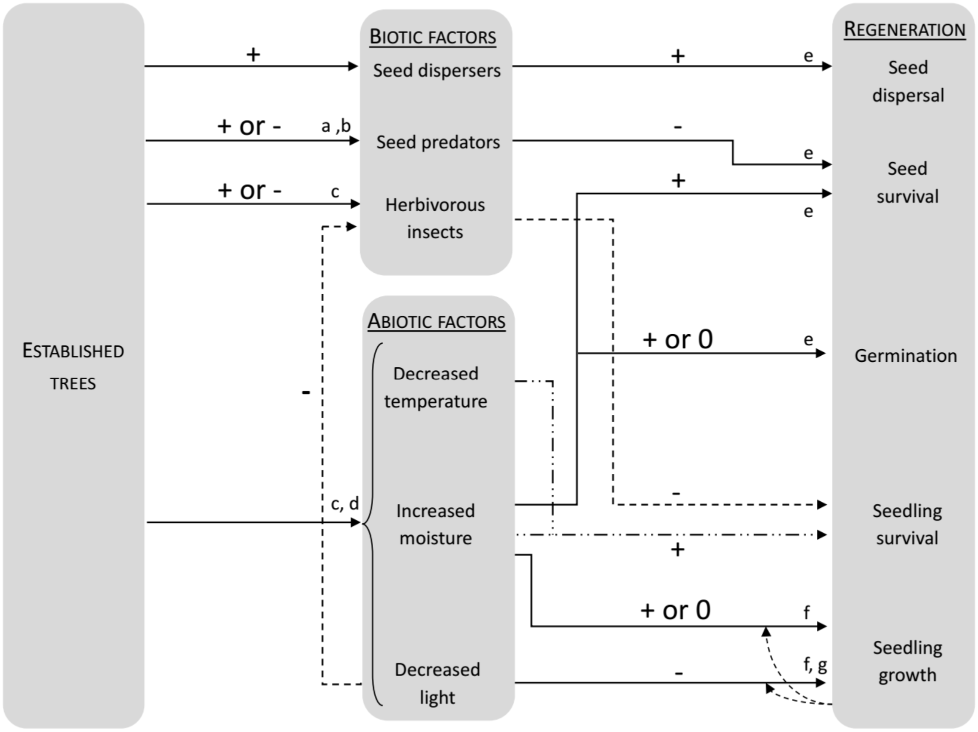

Figure 12. Mechanisms underlying the effect of trees that establish in the early stages of secondary succession on subsequent regeneration of woody plants in tropical dry forests. The plus, minus and zero symbols indicate positive, negative, and absence of effect, respectively. The letters on the arrows refer to the factors influencing the effect considered: (a) successional stage, (b) predator type, (c) leaf phenology of the established tree species, (d) density of canopy cover, (e) seed type, (f) regenerating species, and (g) intensity of shading.

4.1.2 Support for the stress gradient hypothesis

I used logistic regressions to assess the probability that a study would show evidence for a net positive/negative effect of established trees on regeneration as a function of the mean annual rainfall. I found that the probability of a positive effect on seedling survival decreased with increasing rainfall, while the probability of a negative effect increased (Figure 13). This result supports the stress gradient hypothesis, which predicts that facilitation is more important when environmental conditions are particularly harsh (Bertness & Callaway, 1994; Callaway, 1995; Callaway & Walker, 1997). However, my analysis did not support this hypothesis for seedling growth ($p = 0.853$ for net positive effect and $p = 0.862$ for net negative effect). These results are based on a relatively low number of studies; it would therefore be interesting to conduct these analyses again once more studies become available. The low number of studies for the other regeneration stages prevented the stress gradient hypothesis being tested for them.

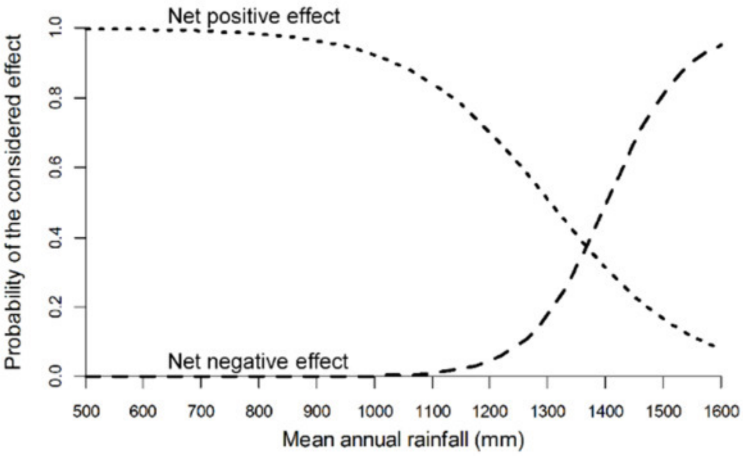

Figure 13. Probability of observing a net positive effect or a net negative effect of established trees on seedling survival as a function of the mean annual rainfall. Models fitted with logistic regressions: positive effect ($p = 0.008$, $R^2 = 0.43$), negative effect ($p=0.009$, $R^2 = 0.56$).

4.2 Changes in species diversity and composition during succession

This section presents and discusses the main results of paper II.

4.2.1 Resilience of species richness and convergence of species composition

Using meta-analysis of studies of the taxonomic changes occurring during succession in tropical dry forest, I found a positive rate of change (the effect size shown by the meta-analysis) in standardised species richness with increasing successional age (Figure 14). This result shows a gradual accumulation of species that is consistent with the trends generally observed in tropical forests (Chazdon *et al.*, 2007; Letcher & Chazdon, 2009; Dent *et al.*, 2013). For the studies that included data for old-growth forests, species richness reached a level similar to that of old-growth forests in 60 years or less, which is consistent with the results of Martin *et al.* (2013) across tropical forests.

Interestingly, the results for evenness obtained with the Shannon evenness and the Simpson evenness indices differed: Shannon evenness index showed an overall significant increase with succession, whereas no significant trend was observed for Simpson evenness index. This difference might be due to the divergence in conceptual opinions about what evenness actually is, as reflected in the differences in the way it is calculated between the two indices (Tuomisto, 2012). While the Simpson evenness index is independent of species richness, the Shannon evenness index is not (Smith & Wilson, 1996; Magurran, 2005; Jost, 2010; Tuomisto, 2012). The trend observed for the Shannon evenness index with succession might therefore result from the trend observed for species richness.

The similarity of species composition with old-growth forests was found to increase with successional age in two separate analyses of the short- and long-duration studies (Figure 14). However, the rate of change was slow and the similarity of successional forests with old-growth forests remained relatively low even after several decades. This result suggests that, although the species composition of secondary forests converges towards that of old-growth forests, there is substantial uncertainty about the recovery of species composition. The recovery of the exact composition of old-growth forests may never happen (Chazdon *et al.*, 2007). However, the low levels of similarity of successional plots with old-growth forests should be interpreted with caution. The size of the sampling area is likely to be too small to encompass all species present in the studied communities, as shown by the fact that for most of the plots, the species accumulation curves do not reach a level value. Part of the dissimilarity between plots could therefore be due to species that are present in the whole communities but not in the plots. There are two possible solutions to this problem. (1) At the data collection stage, the plot size could have been chosen to be large enough to encompass the majority of the species present in the community (as indicated by a levelling of the species accumulation curves). Because I used secondary data for this meta-analysis, this solution was impossible for me to implement. (2) During the data analysis, I could have used a method for estimating the similarity that takes into account the unseen species, such as the abundance-based Chao-Sørensen estimator (Chao *et al.*, 2005). However, the reason why I did not use this index is because there is no occurrence-based equivalent, to the best of my knowledge. Another result that needs to be interpreted with caution is the difference in rates of change of similarity indices for studies of different durations. There is only one study for the shorter duration and the higher rate of change for this study may be idiosyncratic.

Overall, my results show sufficient resilience of species richness to support the potential of secondary forests for long-term biodiversity conservation. Nonetheless, active restoration intervention may still be needed to recover the species composition of old-growth forests.

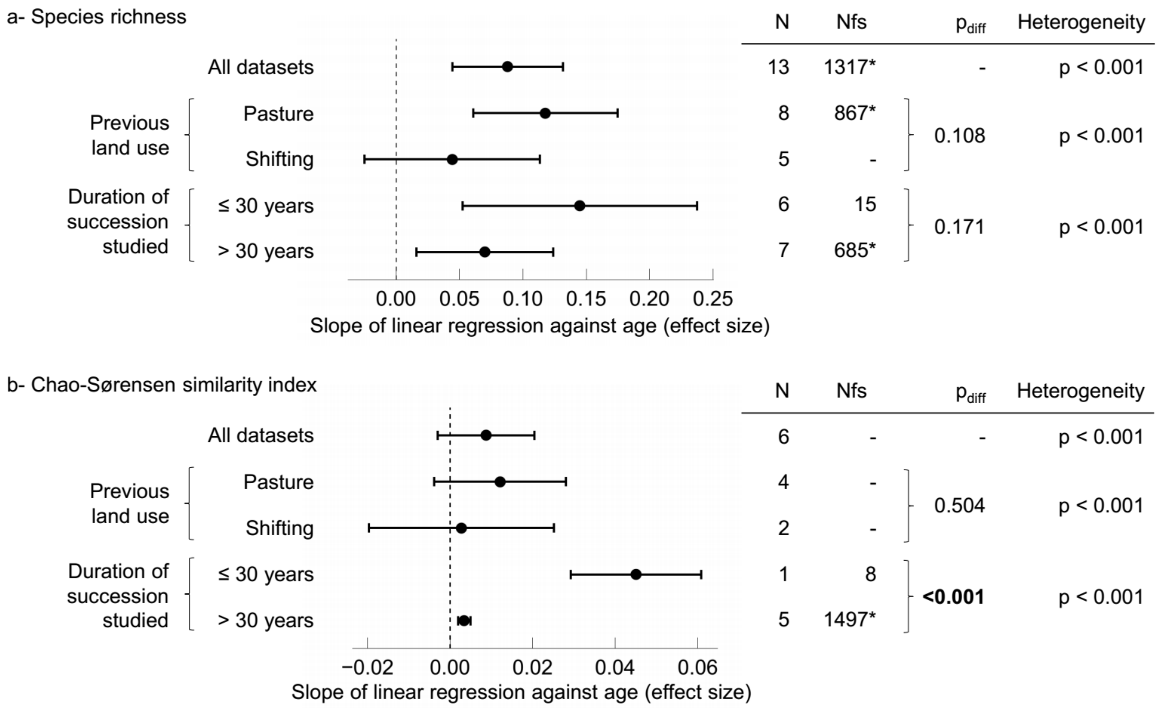

Figure 14. Estimated effect sizes (slope of the linear regression against successional age) of one meta-analysis (all datasets) and two meta-regressions (with previous land use and duration of succession studies) for a) species richness (standardised to 15 individuals) and b) the Chao-Sørensen species composition similarity with old-growth forests. The error bars indicate the 95% confidence intervals. N is the number of datasets for each case. Nfs is the fail-safe number (*i.e.* the number of datasets with null effect that need to be added to lose the significance of the estimated effect size at p = 0.05) for the significant effect sizes. The estimate is robust if Nfs > 5N+10 (indicated with an asterix). p_{diff} is the p-value for the significance of the difference between two modalities of a moderator. Heterogeneity between datasets is tested with the Cochran's Q test for meta-analysis and with the Q-E test for meta-regressions (a significant p-value indicates heterogeneity). Shifting means shifting cultivation.

4.2.2 Factors affecting the rates of changes

I expected a difference between pasture and shifting cultivation land uses in their influence on subsequent succession because of their different effects on the soil and remnant vegetation. However, I did not find any significant differences in the rates of change for the analysed indices between the two previous land uses (except for Shannon evenness index). Similarly, Norden *et al.* (2015) and Poorter *et al.* (2016) did not find any effects of previous land use on changes in forest structure and species density with succession. This absence of correlation can be explained by the heterogeneity within the two land use categories due to differences in the abundance of remnant vegetation, the intensity and duration of the land use, the use of fire and the post-abandonment disturbance regime.

The precipitation regime (mean annual precipitation and number of dry months) and the availability of water (ratio between annual potential evapotranspiration and mean annual precipitation) had no significant effect on the rate of change in the analysed indices. A possible reason is that these variables can have opposite effects on the importance of resprouting and facilitation (Callaway & Walker, 1997; McDonald *et al.*, 2010) and on the size of the species pool capable of tolerating low levels of water availability.

The absence of significant effects of the previous land-use, the precipitation regime and the availability of water should, however, be interpreted with caution because of the low number of studies included in the meta-analyses. It will be useful to conduct these analyses on a larger dataset, once more studies become available.

The heterogeneity of rate of change in species diversity and composition observed could be explained by factors that could not be tested in my meta-analysis, such as the position of successional forests in the landscape (Castillo-Nunez *et al.*, 2011; Chazdon, 2014; Arroyo-Rodriguez *et al.*, 2016), differences in soil properties (Powers *et al.*, 2009) and stochastic events (Norden *et al.*, 2015).

4.3 Isolated trees as nuclei of regeneration in pasture

This section presents and discusses the main results of paper III.

4.3.1 Effect of the surrounding landscape

Most of the properties of the regeneration assemblages below the crowns of isolated trees in pastureland (number of individuals, number of species and functional composition, but not life form) were correlated with at least one of the landscape factors analysed (position of the tree in the landscape relative to patches of trees, measured as a distance and as the area of tree patches in buffers of radius from 100 to 1000 m). These results support the important influence of the surrounding landscape on the re-establishment of forest on agricultural land (Chazdon, 2014). However, the effect of the landscape varied greatly between study sites, suggesting the importance of other landscape factors, such as the wider abundance of scattered trees or live-fences acting as stepping stones and corridors for disperser animals (Estrada *et al.*, 1993; Chazdon *et al.*, 2011).

4.3.2 Effect of isolated trees

Isolated trees differed in their influence on the regeneration assemblage establishing beneath their crown: I found that the functional composition of the regeneration assemblage was clearly associated with the attributes of the isolated trees (Figure 15). However, these attributes only poorly explained the taxonomic composition of the regeneration assemblages, which was very site dependent. These results support the existence of a more general determinism and predictability of successional trajectories when considered through functional composition rather than taxonomic composition, in line with the results of several other studies of succession (Fukami *et al.*, 2005; Alvarez-Anorve *et al.*, 2012; Muniz-Castro *et al.*, 2012; Swenson *et al.*, 2012; Dent *et al.*, 2013; Purschke *et al.*, 2013).

The influence of attributes of isolated trees on the functional composition of the regeneration assemblage beneath their crowns can be explained by two mechanisms:

- Amelioration of environmental conditions: there was a lower proportion of individuals having traits associated with tolerance of drought and heat (deciduous and compound-leaved) in the regeneration assemblage under trees able to cast more shade (wider crowns and evergreen leaf phenology). Increased shade leads to a decrease in air temperature and an increase in air humidity and soil moisture (Rhoades *et al.*, 1998; Callaway, 2007), allowing less drought-adapted species to establish.
- Attraction of seed dispersal agents: the analysis predicted that, excluding individuals conspecific with the tree above, 1.3 times more zoochorous individuals regenerate under a zoochorous tree than under an anemochorous tree. This result supports the importance of the seed dispersal type of a tree for its capacity to attract seed dispersers (Da Silva *et al.*, 1996; Galindo-González *et al.*, 2003; de la Peña-Domene *et al.*, 2014).

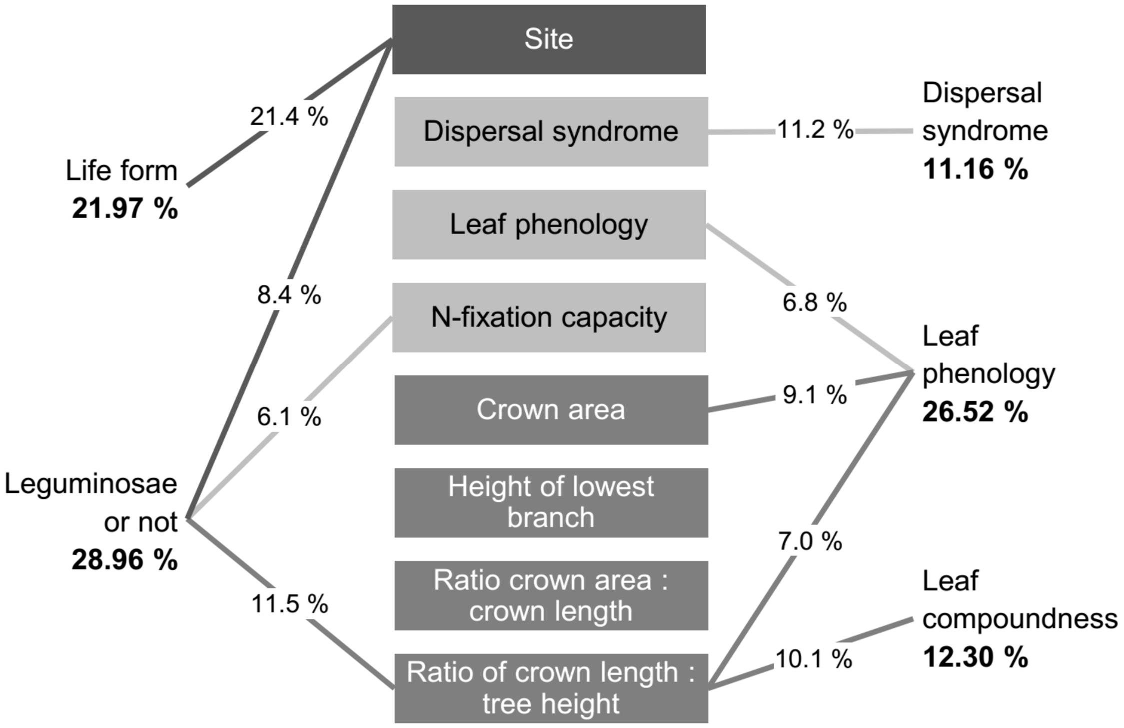

Figure 15. Relationships between the attributes of isolated trees and the functional composition of the assemblages of woody plants regenerating beneath their crowns. The lines indicate all the significant covariates

kept in the best models (attributes of isolated trees, boxes in the centre) with the response variable of these models (properties of the regeneration assemblage, on the sides). The percentage of deviance explained by each model is given in bold below each response variable and the percentage of deviance explained by each isolated tree attribute in a model is given on the line.

4.4 Community assembly during succession

This section presents and discusses the main results of paper IV.

4.4.1 Changes in functional composition with succession

Multi-trait and single-trait analytical approaches both showed directional changes during succession driven by the associated changes in environmental conditions (Figure 16). The changes followed two main trends, the first being by far the most important:

1. A shift from conservative towards acquisitive leaf strategies and a decrease in the proportion of legumes: this trend was associated with decreases in the canopy openness and air temperature measured during the wet season, which is the main growing season. In early succession, with high evaporative demand, conservative leaf-trait strategies reduce leaf heat and transpiration (Poorter & Markesteijn, 2008), while legumes maintain a high rate of resource acquisition through efficient water use (Reyes-Garcia *et al.*, 2012).
2. A decrease in drought-coping strategies (leaf deciduousness and pubescence): this trend was associated with the decreases in canopy openness and air temperature measured during the dry season, during which drought-coping strategies reduce mortality (Poorter & Markesteijn, 2008).

Interestingly, these trends are consistent with other studies carried out in tropical dry forests in Costa Rica (Becknell & Powers, 2014; Buzzard *et al.*, 2015) but contrast with studies carried out in tropical dry forests in Mexico (Lebrija-Trejos *et al.*, 2010b; Lohbeck *et al.*, 2013), suggesting geographical variation of trends in functional composition during succession amongst the spectrum of tropical dry forests.

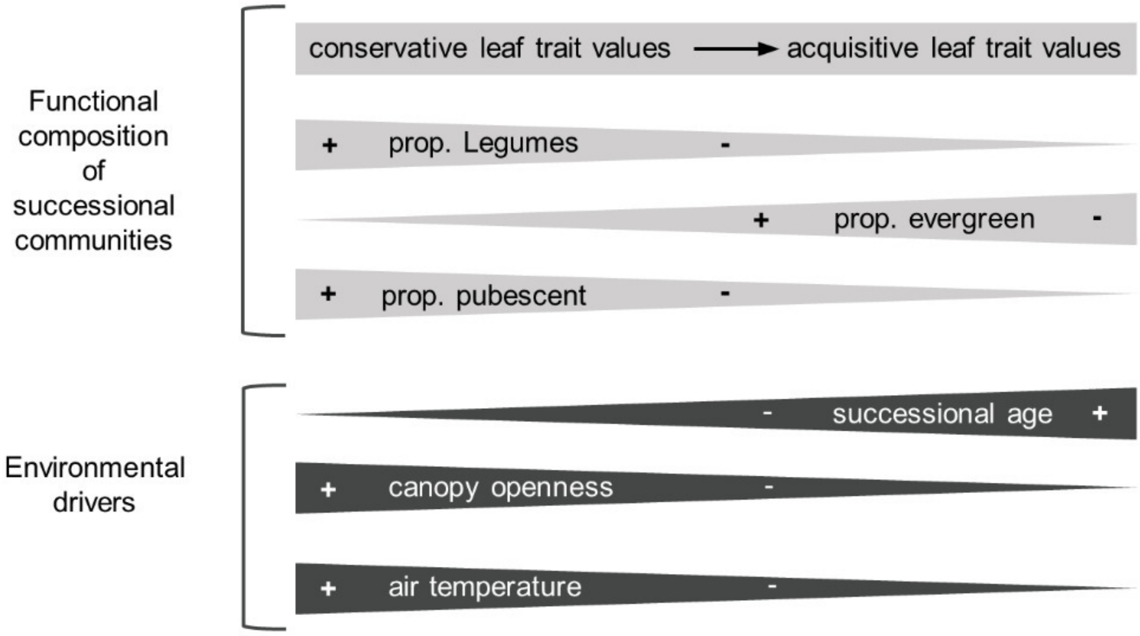

Figure 16. Overview of the changes in functional composition during secondary succession in tropical dry forest and their underlying environmental drivers. Prop. stands for proportion.

4.4.2 Importance of intraspecific variation of functional trait values

Partitioning of the variance of the whole dataset of leaf functional trait values across nested levels ranging from the leaf to the species showed that the variance of most traits was largely explained by between-species differences (on average 71.3% for non-chemical traits and 60.7% for chemical traits) (Figure 17). The amount of intraspecific variation was, however, not negligible. In paper IV, I consider this intraspecific variation, focusing on its importance in explaining changes in functional composition of communities in response to successional gradients and on intraspecific changes with ontogeny.

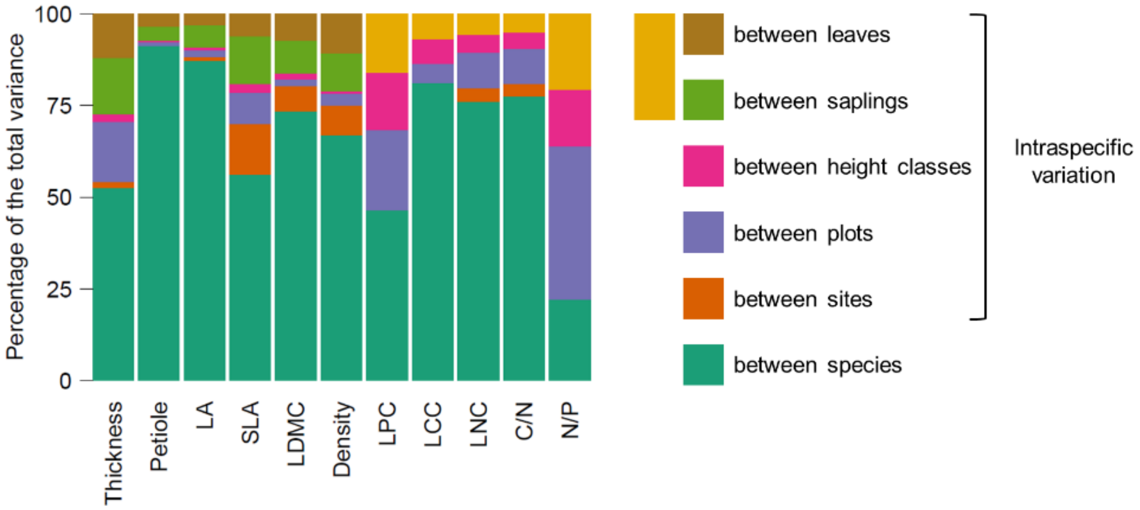

Figure 17. Partitioning of the variance of traits across nested levels of organisation (performed on 2539 leaves, 852 individual saplings, 69 species). Thickness stands for leaf thickness, Petiole for petiole length, LA for leaf area, SLA for specific leaf area, LDMC for leaf dry matter content, Density for leaf density, LPC for leaf phosphorous concentration, LCC for leaf carbon concentration, LNC for leaf nitrogen concentration, and C/N and N/P are leaf stoichiometric ratios.

Intraspecific variation along the successional gradient

Both analytical approaches (multi- and single-trait) showed that the contribution of species turnover was more important than intraspecific variation in explaining the changes in community trait values during succession. However, the changes in community trait values that occur through intraspecific variation were strongly associated with the changes in environmental conditions during succession. This confirms the directionality of changes in trait values within species along environmental gradients found in other contexts (Lepš *et al.*, 2011; Bhaskar *et al.*, 2014; Carlucci *et al.*, 2015) and suggests a plastic response of trait values to environment. The response of community trait value through intraspecific variation was particularly important for morphological and chemical traits associated with leaf economics.

Intraspecific changes due to ontogeny

Five of the 11 continuous traits studied showed a directional change with ontogenic stage (using the proxy of sapling height divided by maximum height of the species): increase of leaf thickness, density, LDMC and LCC and decrease of SLA. This suggests a change from acquisitive to conservative strategies with ontogeny. If this trend extends beyond the short ontogenic window considered, as found by studies in other forest biomes (Thomas & Winner, 2002; Niklas & Cobb, 2008; Spasojevic *et al.*, 2014), this means that a tree growing in the successional forests studied would experience opposing changes due to succession (conservative to acquisitive) and ontogeny (acquisitive to conservative). Dynamic studies over larger ontogenic windows are needed to resolve the net outcome of these opposite changes.

4.5 The influence of changing abiotic and biotic environmental conditions during succession on the fate of seeds

This section presents and discusses preliminary results of the study of seed fate. I used GLMs to assess the influence of the site (intermediate-aged *versus* young secondary forest *versus* open area), litter treatment (with or without litter), predation treatment (with or without protection against predation) and species (seven) on two types of seed fate:

- seed removal, being the disappearance of a seed from the cluster, measured two weeks after the beginning of the experiment as a proportion of the number of seeds initially placed in the cluster (after two weeks, the difficulty of relocating seeds made the assessment of this fate unreliable),
- seed germination, measured 12 weeks after the beginning of the experiment as the proportion of the number of seeds present at week two, which was the time of the first rain since the start of the experiment.

Characteristics of the seven studied species are presented in Appendix 1, characteristics of the three studied sites in Appendix 2 and the effect of the litter treatment and of the site on microclimatic conditions in Appendix 3.

4.5.1 Influence on seed removal

Model selection using the Akaike information criterion (AIC) resulted in a model with the site, the litter treatment, the predation treatment, the species and the interactions site * predation treatment, site * species, litter treatment * species and predation treatment * species (Table 2).

The presence of litter resulted in a large and significant decrease in seed removal, across species and for five of the seven species. This result is in line with the results of Cintra (1997) and suggests that leaf litter protects seeds by reducing the probability that they will be located by seed predators. Interestingly, the presence of litter was much more important in reducing seed removal than the treatment of protection from predation with a wire mesh, which was only significant in young forest and for the big-seeded species *Hymenaea courbaril*. The mesh of the wire used for this treatment (1.27 cm) excluded most vertebrates but not most insects that can remove small seeds (such as seeds of *Cochlospermum vitifolium* and *Stemmadenia obovata*, personal observation).

Seed removal was significantly higher in the intermediate-aged than in the young secondary forest and the open area when considered across species and for three species (*Astronium graveolens*, *Dalbergia retusa* and *Simarouba amara*) individually. This result is consistent with those of Wassie *et al.* (2010) and Souza-Silva *et al.* (2015), who found more predation under closed canopies, and suggests that there is a higher abundance of seed predators in intermediate-aged forests. Birds and rodents have been shown to frequent open sites less often (Da Silva *et al.*, 1996; Vieira & Scariot, 2006a). Consistently with the results of Vieira and Scariot (2006a), the effect of the site was dependent on the species: for *Hymenaea courbaril*, which is mainly predated by rodents (Asquith *et al.*, 1999), seed removal is significantly lower in the younger forest whereas for *Stemmadenia obovata*, mainly dispersed by birds, removal was significantly higher in the younger forest.

Although the responses to site and to litter and predation treatments was species-dependent, they do not seem to be related to seed size, presence of a hard coat, dispersal syndrome or successional status (Appendix 1). These traits are therefore inadequate proxies to enable understanding of the importance and type of predation and secondary dispersal, at least for the limited number of species that I studied.

Because I did not study the fate of the seeds after removal from the cluster, I cannot consider that the removed seeds have necessarily been predated. For some of the tested species, such as *Hymenaea courbaril*, scatter hoarding and seed burial by predators is known to be important and can lead to seed germination after secondary dispersal (Asquith *et al.*, 1999; Cole, 2009).

Table 2. *Result of the selected GLM testing the response of the proportion of seeds that were removed to the experimental treatments. The values presented are the difference between the proportion estimated by the model for two categories of each treatment. Since all the explanatory variables are categorical, the values presented indicate the importance of the treatment effect. Significance tests are performed on the linear-predictor scale. Effects with a p-value* < 0.001 *are shown as ***,* $p < 0.01$ *as **,* $p \leq 0.05$ *as * and* $p > 0.05$ *as ns (non-significant). Significant effects are shown in bold. Species names are given in full in section 3.2.3, inter. stands for intermediate-aged secondary forest.*

Treatment	Relative effect across species	per species						
		Astronium	*Cochlospermum*	*Dalbergia*	*Hymenaea*	*Simarouba*	*Stemmadenia*	*Thouinidium*
Litter treatment (with litter - without litter)								
overall	**-0.161** ***							
per species		-0.020 ns	**-0.373** ***	**-0.550** ***	**-0.103** **	-0.022 ns	**-0.164** *	**-0.088** *
Predation treatment (with protection - without)								
overall	-0.026 ns							
per site								
inter.	-0.092 ns							
young	**-0.037** *							
open	0.026 ns							
per species		-0.011 ns	-0.046 ns	0.079 ns	**-0.113** **	-0.038 ns	0.011 ns	-0.010 ns
Site								
overall								
inter - young	**0.194** ***							
inter - open	**0.176** ***							
young - open	-0.019 ns							
per species								
inter - young		**0.215** *	-0.039 ns	**0.691** ***	**0.190** *	**0.283** **	**-0.409** ***	0.093 ns
inter - open		**0.260** **	-0.100 ns	**0.672** ***	-0.043 ns	**0.276** **	0.060 ns	0.088 ns
young - open		0.045 ns	-0.061 ns	-0.019 ns	**-0.233** *	-0.007 ns	**0.469** ***	-0.005 ns

4.5.2 Influence on seed germination

Model selection for seed germination retained site, litter treatment, predation treatment, species and the interactions site * litter treatment, litter * predation treatment and litter treatment * species (Table 3).

Site (two ages of secondary forest or open area) was the treatment with the largest significant effect on seed germination. There was a higher germination rate in the two forests sites compared with the open site, consistent with previous results in tropical dry forests (Hardwick *et al.*, 1997; Alvarez-Aquino *et al.*, 2014). This can be explained by the canopy shade reducing air and soil temperature and increasing air humidity (Appendices 2 and 3), as suggested by studies using artificial shading and watering (Hardwick *et al.*, 1997; McLaren & McDonald, 2003a). Moreover, this amelioration of microclimate can reduce seed mortality by desiccation (Vieira & Scariot, 2006a).

The presence of litter had significantly positive overall effect on seed germination. This can be explained by the significantly higher air humidity and lower soil temperature under the litter (Appendix 3). However, the effect of the presence of litter was dependent on the site: it was only significant in the younger forest. In the open site, the litter was very thin and composed only of dry thatch remnants of the previous year's herbaceous vegetation. Its low effect on microclimatic conditions is probably not important enough to mitigate the hot and dry conditions of this site (Appendices 2 and 3). On the contrary, in the intermediate-aged forest, the relatively high humidity and low temperature provided by the canopy can be favourable enough for germination so that litter does not have an additional effect. The effect of the presence of litter was also species-dependent: it was only significantly positive for *Dalbergia retusa*, *Simarouba amara* and *Thouinidium decandrum*. As for seed removal, the analysed seed traits, dispersal syndrome and successional status did not explain the species-specific response to litter treatment.

The protection against seed predation had a positive effect on seed germination, both overall and through its interaction with the litter treatment. This effect is likely to be due to the fact that the reduced seed removal leaves more seeds able to germinate. In the same way, part of the observed effect of the presence of litter on the germination rate may be due to an indirect effect on seed removal.

Treatment	Relative effect	
<u>Litter treatment (with litter - without litter)</u>		
overall	**0.064**	*
per site		
intermediate forest	0.019	ns
young forest	**0.151**	***
open site	0.028	ns
per predation treatment		
with protection	0.023	ns
without protection	**0.088**	**
per species		
Astronium graveolens	- 0.064	ns
Cochlospermum vitifolium	0.006	ns
Dalbergia retusa	**0.187**	**
Hymenaea courbaril	-0.008	ns
Simarouba amara	**0.180**	**
Stemmadenia obovata	0.011	ns
Thouinidium decandrum	**0.257**	***
<u>Site</u>		
overall: intermediate - young forest	0.020	ns
overall: intermediate forest - open site	**0.204**	***
overall: young forest - open site	**0.184**	***
<u>Predation treatment (with protection - without)</u>		
overall	**0.103**	***

Table 3. *Result of the selected GLM testing the response of the proportion of seeds that germinated to the experimental treatments. The values presented are the difference between the proportion estimated by the model for two categories of each treatment. Since all the treatment variables are categorical, the values presented indicate the importance of the treatment effect. Significance tests are performed on the linear-predictor scale. Levels of significance are indicated as in Table 2.*

5 General discussion

5.1 Predictability of successional trajectories

I found that successional trajectories in tropical dry forests are quite unpredictable when taxonomic composition is considered. In paper II, I showed that the convergence of species composition of successional tropical dry forests towards the composition of old-growth forests is slow and the similarity of composition between successional and old-growth forests remains low even after several decades of succession. In paper III, I showed that the species composition of the assemblages of woody species regenerating under the canopy of isolated trees in pasture was poorly explained by the attributes of these trees. On the contrary, attributes of isolated trees explained relatively well the functional composition of the regeneration assemblage. Paper IV showed the directional changes in functional trait values of sapling communities during succession. These results support the hypothesis of a higher predictability of successional trajectories when considered in term of functional traits than taxonomic composition. Previous studies also found evidence supporting this hypothesis: for example, Dent *et al.* (2013) showed that successional tree communities in tropical moist forests increased in similarity with old-growth forests when considering species' shade tolerance but not species composition. Fukami *et al.* (2005) found a divergence in species composition but a convergence of functional group composition over time in experimental grassland.

This higher predictability of functional than taxonomic composition during tropical dry forest succession can be explained by the overlap of niches and of functional trait distributions of species (Violle *et al.*, 2012). Indeed, even if it is well established that species differ in their environmental requirements (contrary to the hypothesis of functional equivalence proposed by the neutral theory of Hubbell, 2005), species niches are not totally disjunct and a high number of species can establish and thrive in the same environment. This is the idea of functional redundancy of species that, although mainly developed for the effect of species on their environment and the consequences for ecosystem functioning and conservation (Walker, 1992; Diaz & Cabido, 2001), can also be viewed in term of species response to their environment (Diaz & Cabido, 2001). While the functional traits of plants in a community are filtered by the abiotic and biotic environment, the identity of the species that successfully establish in successional forests is locally dependent on their presence in the surrounding landscape and their ability to be dispersed, and on stochastic events affecting their dispersal and establishment.

The higher predictability of changes in functional than taxonomic composition highlights the interest of considering community assembly through the lens of functional composition to get a better understanding of its drivers. When doing so, it is important to go back to the definition of functional trait, *i.e.* a “feature measurable at the level of the *individual*” (Violle *et al.*, 2007), and to take into account the variation of functional trait values within species, as an increasing number of ecologists advocate (Lepš *et al.*, 2011; Violle *et al.*, 2012; Laughlin & Messier, 2015)[9]. Increasing evidence for the importance of intraspecific variation of functional trait values compared with their interspecific variation shows the limit of an approach based on mean trait value per species (Hulshof & Swenson, 2010; Messier *et al.*, 2010; Siefert *et al.*, 2015). Mean values cannot take into account the plasticity of trait values within species in response to environmental conditions and therefore cannot inform on the importance of niche-overlap among species (Laughlin & Messier). Several studies have shown the importance of intraspecific variation of trait values in the response of communities to environmental gradients (Lepš *et al.*, 2011; Carlucci *et al.*, 2015), but the study presented in paper IV is the first, to the best of my knowledge, to do so for a successional gradient. It showed that, for some traits, the association between community trait values and environment was stronger (or even only detected) when considering intraspecific variation.

The study presented in paper IV showed that, besides their changes with environment, trait values also vary within species with ontogeny, as evidenced by previous studies (Thomas & Winner, 2002; Niklas & Cobb, 2008; Spasojevic *et al.*, 2014). To embrace the full range of trait values within species, appropriate sampling protocols are required (Violle *et al.*, 2012). Exhaustive sampling strategies such as the one I carried out for paper IV are time-consuming and therefore expensive (Baraloto *et al.*, 2010a). This generally result in a trade-off between the number of individuals per site and species and the size and number of plots that can be studied. Sampling strategies therefore need to be carefully fitted to the processes and mechanisms targeted by the study and to the variability of the traits considered.

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[9] See also the post of Brian McGill on the blog *Dynamic ecology* (https://dynamicecology.wordpress.com/2015/07/01/steering-the-trait-bandwagon/)

5.2 Difference in successional trajectories between tropical dry forests

Several of my results show or suggest that successional trajectories are not similar in all tropical dry forests. Here I discuss these results within the framework of the conceptual model presented in the introduction (Figure 1) and consider the influence of regional abiotic factors, landscape factors, past and present land uses and remnant vegetation on successional trajectories in tropical dry forests.

Tropical dry forests are encountered within a wide range of climatic conditions (see definition of tropical dry forests in section 1.5.1). This gradient, and especially climatic factors directly related to water availability, is expected to explain part of the heterogeneity of successional trajectories in tropical dry forests. Several of my results support this hypothesis. Paper I shows that the importance of positive and negative effects of established trees on the survival of seedlings beneath their crowns depends on the mean annual rainfall. The changes in plant strategies with succession observed for the tropical dry forests of Costa Rica (paper IV and Becknell and Powers, 2014; Buzzard *et al.*, 2015) differ from those observed in tropical dry forests of Mexico (Lebrija-Trejos *et al.*, 2010b; Lohbeck *et al.*, 2013). These two areas are at the opposite ends of the tropical dry forest climate gradient, with mean annual rainfall of ~ 1700 mm in Costa Rica and 900 mm in the Mexican site. This suggests that the trends of change in functional strategies during succession can vary along a gradient of precipitation within the range of tropical dry forests, although studies in other sites are needed to substantiate this hypothesis. The results of paper II, on the contrary, do not show support for the influence of the climatic gradient on successional trajectories, as indicated by species diversity and composition, even when assessing water availability, which is a more integrative index of climate than precipitation. Species diversity and composition are indices that ultimately result from several interacting mechanisms. Studying the changes in mechanisms and processes other than the ones tested in papers II and IV, by Becknell *et al.* (2012) (change in aboveground biomass) and by McDonald *et al.* (2010) (relative importance of seed *versus* vegetative reproduction) would allow the climatic categorisation of tropical dry forests to be refined. Interestingly, paper I and McDonald *et al.* (2010) both identified a possible switching point around 1400 mm of mean annual rainfall and Becknell *et al.* (2012) found that tropical dry forests with more than 1500 mm had a greater rate of biomass accumulation during succession compared with drier forests. Conversely, considering the gradient of climatic conditions from dry to wet tropical forests could be a good alternative for functional ecology to their categorical classification.

The influence of landscape factors, past and present land uses and remnant vegetation on successional trajectories needs to be studied further. Paper II did not find any influence of previous land use on the rates of change in species richness or composition during succession. Paper III found that the effects of landscape factors were complex and site-dependent. Landscape and land-use factors are difficult to measure and the complexity of their effects cannot easily be synthesised in simple quantitative or qualitative indices. For example, the reporting of past-land uses by the studies reviewed in paper II did not give any quantitative and standardised information on the use of fire or the intensity of the past land use (*e.g.* in terms of intensity of grazing or number of cultivation cycles). Paper III shows that not only the presence but also the attributes of isolated trees in pasture influence the regeneration of woody species. Scaling up the results of individuals studies to wider spatial or temporal scales is therefore problematic. Despite these methodological challenges, the inclusion of more detailed landscape and land use factors in analysis of succession would improve understanding of their influence on successional trajectories (Chazdon, 2003; Chazdon *et al.*, 2007).

5.3 Implication for ecological restoration of tropical dry forests

When planning an ecological restoration project, the first step is to identify the objectives of the restoration and the opportunities and constraints of the site to be restored (Griscom & Ashton, 2011; Holl & Aide, 2011). In many cases, passive restoration, based only on natural regeneration, can be a valuable and relatively low-cost option when the objective is to recover a functional ecosystem with a high level of biodiversity. Paper II showed that secondary tropical dry forests have good resilience of their shrub and tree species richness and can reach levels of richness similar to those of old-growth forests in a few decades. Other studies have shown that this is also the case for aboveground biomass (Becknell *et al.*, 2012; Poorter *et al.*, 2016). In paper III, I found 126 species of trees, shrubs and lianas regenerating in three active pasture sites, which would be a promising starting point once the farming activity is abandoned. More generally, the *Área de Conservación de Guanacaste* where I carried out my fieldwork is a very good example of a successful restoration programme mainly based on passive restoration (Janzen, 2002; Aronson *et al.*, 2005).

With respect to the opportunities and constraints of an area to be restored, it is important to assess the composition and abundance of the vegetation within and in the surroundings of the site. Paper III confirmed the importance of the presence of isolated trees within the site to facilitate regeneration (Guevara *et al.*, 1986; Schlawin & Zahawi, 2008; Griscom & Ashton, 2011). It also showed the importance of vegetation patches in the surroundings as seed sources and suggested the importance of scattered trees, living-fences and riparian vegetation to maintain connectivity within the landscape by acting as stepping stones and corridors for animal dispersers (Chazdon, 2014). Fire, grazing or the presence of vegetation limiting succession (such as invasive grasses planted in tropical pastures, Griscom & Ashton, 2011) are potential barriers to restoration. I have not studied these constraints in detail but I discuss them in paper II. When these constraints are present, intervention may be needed to remove them, as it is the case in the *Área de Conservación de Guanacaste* (Janzen, 2002).

With passive restoration, however, there is important uncertainty about the species composition of successional forests and their capacity to recover the full woody plant species composition of old-growth forests (paper II). If the objective of restoration is to re-establish a particular set of species, active restoration techniques (through sowing or planting) may be needed. Such intervention can also accelerate the re-establishment of the forest (Griscom & Ashton, 2011). In tropical dry forests, tree cover (continuous or in isolated trees or patches) has an overall positive effect on regeneration by attracting seed dispersers and mitigating harsh climatic conditions, and therefore increasing the establishment and survival of young woody plants (papers I and III and seed study). Species used for active restoration need to be carefully selected. Paper III showed that the attributes of the trees forming the first cover at the early stage of succession influence the composition of the assemblage of woody plants regenerating subsequently, hence suggesting a long-term legacy of the composition of the early stages. An approach based on functional traits can be valuable to guide the choice of species (Martínez-Garza *et al.*, 2005; Ostertag *et al.*, 2015). Paper IV suggests that species with conservative values of leaf traits can cope better with the open and hot environment of early succession, at least in the tropical dry forests of Costa Rica. Species with such leaf traits are therefore good candidates for active restoration. Legumes, which are abundant in tropical dry forests (Gentry, 1988), are also an interesting option: besides being able to thrive in the microclimatic conditions of the early stages of succession, many species are also able to fix nitrogen (Corby, 1988).

Selecting evergreen species has the advantage of providing shade even during the dry season and hence reducing the mortality risk for young woody plants establishing underneath (paper I). Paper III also showed that evergreen trees can foster the establishment of a larger number of species under their crowns. However, evergreen species are naturally less abundant in the early stages of succession and can be more sensitive to desiccating environmental conditions (paper IV).

Once the canopy cover is closed and the microclimate changes towards more shaded, cool and moist conditions, species with more acquisitive leaf trait values should start establishing. If this is not the case, it could be a sign of dispersal limitation for these species and enrichment planting might be needed.

6 Critical assessment and future research

6.1 Critical assessment of my PhD research

Two papers (I and II) are based on a systematic review of the scientific literature. The relatively low number of studies included in these reviews (29 studies in paper I and 13 datasets from 9 studies in paper II[10]) confirms that the tropical dry forest biome receives relatively less attention from scientists than other tropical forest biomes and that more studies are needed (Sanchez-Azofeifa *et al.*, 2005; Vieira & Scariot, 2006b; Quesada *et al.*, 2009). The qualitative and quantitative analyses conducted in papers I and II would need to be renewed once more studies become available. For paper I, the low number of studies was one factor preventing the use of a meta-analysis approach. The analysis conducted to test the stress gradient hypothesis is a vote-counting approach, an approach less powerful than a meta-analysis because it does not enable an overall effect-size to be calculated and the studies to be weighted by their precision (Koricheva & Gurevitch, 2014). Extending this analysis to the whole climatic range of tropical forests would likely have led to the inclusion of a larger number of studies enabling the use of a meta-analysis, but at the cost of reducing the paper's focus on tropical dry forests. For paper II, however, the number of studies included was sufficient to get very robust results (as shown by the fail-safe numbers). Papers I and II also showed an unbalanced distribution of the research effort between tropical dry forest regions. Sixty-nine per-cent of the studies included in paper I and 92% of the datasets included in paper II were conducted in the Neotropics, whereas Miles *et al.* (2006)[11] estimate that 67% of tropical dry forests are located in this region. This is consistent with research showing an overall unbalanced distribution of ecological studies in the tropics (Stocks *et al.*, 2008; Powers *et al.*, 2011). The results of these two papers, and especially paper II, should be

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[10] The inclusion of a study in the meta-analysis conducted in paper II was dependent on the availability of raw data. The number of studies that could potentially have been included, but for which I did not manage to contact the authors or I did not get the agreement to use the data, was roughly ten.

[11] See section 1.5.1 for details on the methods used in this study.

considered with caution for African and Asian dry forests where the size of the species pool, floristic composition, disturbance history and forest fauna differ (Corlett & Primack, 2006; Dexter *et al.*, 2015; Slik *et al.*, 2015).

Two main observational approaches are used to study succession in forests: the dynamic approach monitoring the changes occurring in permanent plots over time, and the chronosequence based on a space-for-time substitution (Chazdon, 2014). The long temporal scale of succession in forests makes the former approach more difficult and hence less commonly used in tropical forests (Chazdon *et al.*, 2007; Chazdon, 2014). Several studies in this thesis are based on a chronosequence approach (papers II and IV, and the study of seed fate). This approach has potential biases. The environmental conditions of the study sites at the beginning of secondary succession and history of land use are usually difficult to know with accuracy, which results in a risk of wrongly attributing to an effect of succession differences that are simply due to variation amongst sites (Pickett, 1989; Chazdon, 2014). Moreover, there is possible confounding between site conditions and time of abandonment (Chazdon, 2003): for example, agricultural activities are likely to be abandoned in less fertile sites earlier than in more fertile ones. Several studies have used a combination of chronosequence and dynamic approaches (over less than 10 years) to test if the predictions resulting from analysis of chronosequences match those of the dynamic approach. Maza-Villalobos *et al.* (2011a) found that neither the trends observed for forest structure, nor for species diversity, with the chronosequence approach were consistent with those of the dynamic approach. Chazdon *et al.* (2007) showed that predictions related to forest structure were better than those of species diversity, while Mora *et al.* (2015) showed the opposite, and Lebrija-Trejos *et al.* (2010a) found that both were well predicted. To the best of my knowledge, no such studies have been conducted to test the validity of the chronosequence approach for changes in functional diversity or composition. Because of the higher predictability of changes in functional than taxonomic composition (see section 5.1), the chronosequence approach can be expected to perform better for changes in functional composition. Despites its limitations, the chronosequence approach is recognized as a useful and pragmatic approach for assessing long-term trajectories of succession (Quesada *et al.*, 2009; Lebrija-Trejos *et al.*, 2010a), as it is the case in paper II.

A strength of my field-based studies and a way to mitigate part of the limitation of the chronosequence approach is the measurement of environmental factors in successional plots. For paper IV and the study of seed fate, I measured microclimatic conditions in each successional plot (see section 3.2.4 for details). The changes in microclimatic conditions are often assumed but rarely measured in successional studies (but see Lebrija-Trejos *et al.*, 2011). Measuring these factors allows a more direct test of their effects on the observed changes in plant communities with site successional age. For paper IV, I also included measurements of soil physical and chemical factors. These factors were generally not significantly correlated with successional age, which shows that there is limited risk of confounding between environmental conditions and successional age. For paper III, measuring microclimatic conditions under isolated trees would have enabled the effects of isolated tree attributes on regeneration through amelioration of environmental conditions to be tested more directly. However, because of the need to take repeated measurements at different times of the day and year to correctly assess microclimatic factors, this approach was impractical given the large number of isolated trees studied.

Soil factors, frequency and intensity of fire events, grazing and competition with exotic grasses are important factors affecting secondary succession (as reviewed in section 1.2.2) but are not a major focus of my study. Soil factors are considered in paper IV through the separation of the two forest types (which differed in soil factors) in the statistical analyses and the results showed the differences in their effects on community functional trait values of the sapling communities. In the study sites of paper IV and the study of seed fate, and more generally in the *Área de Conservación de Guanacaste*, efficient control of fire and exclusion of grazing are implemented as a way of allowing natural succession (Janzen, 2002) and are therefore not a major constraint, at least within the limits of the protected area. The differences observed in regeneration assemblages among the three pasture sites studied in paper III are likely to result partly from differences in grazing intensity, fire history and intensity of the competition with established grass vegetation. However, the high number of individuals and species surveyed (including a high proportion with a height exceeding that of the grass cover) suggests that the effect of these factors is not strong enough to inhibit woody plant regeneration.

The functional traits measured in paper IV are commonly used in ecological studies and their association with resource economics and tolerance of dry and hot conditions is well established (Wright *et al.*, 2004; Poorter & Markesteijn, 2008; Reich, 2014). However, they are all leaf morphological, chemical or phenological traits which are only indirectly related to the function of interest (they are sometimes qualified as “soft traits”, Violle *et al.*, 2012). The measurement of physiological traits directly associated with the functions of interest for the study (“hard traits”), such as photosynthetic capacity and leaf dark respiration rate for resources economics, and C-isotope composition and leaf water potential for drought tolerance (Wright *et al.*, 2004; Markesteijn *et al.*, 2011; Perez-Harguindeguy *et al.*, 2013), would have been valuable. I did consider measuring some of these traits. However, besides the logistical difficulties of accessing equipment and consumables in the field, the time required to measure these traits reliably was not compatible with the extensive sampling design of this study. For leaf phenological traits (included in papers III and IV), I used a coarse categorisation of leaf phenological habit based on expert knowledge. However, species range along a continuum of phenological behaviour (Borchert, 1994) and categorisation is a simplification. Accurately assessing leaf phenological behaviour requires regular (at least-monthly) monitoring of several individuals per species over several years, which was incompatible with the time frame of my PhD research. Such information is available for a number of species in my study area (Borchert, 1994), but not for enough of them to be useful for community studies.

The hypothesis of phylogenetic conservatism predicts that species conserve the ecological characteristics of their ancestors (Ackerly, 1999; Mouquet *et al.*, 2012). Evolutionary close species are therefore expected to have closer values of traits than expected by chance (the phylogenetic signal). As a consequence, species should not be considered as independent for analysis of trait associations, and statistical methods taking into account the phylogenetic signal should be used, such as the phylogenetically independent contrast method (PIC, Felsenstein, 1985). However, I did not use such a method when looking at traits associations to assess plant strategies (appendix D in paper IV), which leads to a risk of confounding bias by evolutionary relationships between species. However, for 87 species of the same study area, Powers and Tiffin (2010) did not find any strong phylogenetic signal in functional trait data, once species of the Leguminosae family were excluded. Similarly, Pringle *et al.* (2011) did not find a phylogenetic signal in 30 species of Mexican tropical dry forests. At the community scale, most studies do not support the hypothesis of a correlation between functional and phylogenetic diversity (Garnier *et al.*, 2016), suggesting a decoupling of functional and phylogenetic structures of communities.

Lastly, time constraints have imposed some trade-off in methodological choices. For example, I would have liked to be able to include more plots for paper IV to improve statistical power, but the necessity to sample a large number of individuals per species and per plot to assess the intraspecific variation prevented that. For the experimental study of seed fate, using a larger number of species may have enabled trends associated with seed traits to be detected.

6.2 My short-term research priorities

Building on the results of my doctoral work, there are several research ideas that I would like to develop. In the immediate future, I plan to work on two studies for which I have already collected data during my PhD:

- To study the influence of established trees and of changing environmental conditions during succession on the growth and survival of seedlings, I have set up an experiment similar to the study of seed fate. I planted seedlings of six species in the two successional forests and applied two treatments (presence or absence of litter and exclusion of root interactions through trenching). I monitored the survival and growth of these seedlings from 2013 to 2015. I measured microclimatic factors in every plot. In 2015, I measured a set of traits (leaf, stem and root) on several individuals per species and per plot. I plan to analyse these data with four main objectives: (1) identify the mechanisms through which established trees influence regeneration, (2) identify the establishment strategies of the studied species (in terms of the potential trade-off between growth and survival), (3) understand the link between functional traits and establishment strategies, considering variation between and within species, and (4) test for a possible effect of abiotic and biotic environmental conditions on intraspecific variation in functional trait values.
- For paper IV, I worked in permanent plots of the research group of Dr Jennifer Powers (University of Minnesota). For these twelve plots and six additional ones, Jennifer Powers' team have surveyed all adult trees and have data on the seed rain and soil seed bank. I also surveyed the saplings and seedlings. We now intend to analyse these data together to study the changes in species and functional composition (using basic traits such as dispersal syndrome and leaf phenological habit) across successional and life stage gradients with the objective of assessing the directionality of these changes and identifying the life stages (from seed dispersal to adult stages) that are the most critical for tree establishment.

In a relatively longer term, there are several ideas I would like to explore:

- Building on paper IV, I would like to further study the intraspecific variation of functional traits with ontogeny and environmental conditions and the importance of intraspecific variation for fitness of plant species and community assembly processes along environmental gradients.

- I would also like to go beyond the leaf economics spectrum and contribute to the timely question of the existence of a spectrum of strategies at the scale of whole plants (Baraloto *et al.*, 2010b; Reich, 2014). I would be interested to study the patterns of correlation of leaf, stem and root traits to understand the response of individual plants and tree communities to changes in their environment and the resulting effects on ecosystem processes.
- Expanding on papers II and IV and the work of Lohbeck and colleagues (Lohbeck *et al.*, 2013; Lohbeck *et al.*, 2015), I would like to use a meta-analysis approach to study if the directionality of change in resource acquisition strategies (considering the more commonly studied traits such as SLA and leaf phenological habit) during succession varies along the precipitation gradient in tropical forests. I would test the hypothesis that at the extreme dry end of the gradient of precipitation, the main axis of change is related to drought-coping strategies (Lebrija-Trejos *et al.*, 2010b; Lohbeck *et al.*, 2013; Lohbeck *et al.*, 2015), then moves to a change from conservative to acquisitive strategies at the upper end of the range of tropical dry forests (Becknell and Powers, 2014; Buzzard *et al.*, 2015 and paper IV) and finally switches to a change from acquisitive to conservative strategies in tropical wet forests (Lohbeck *et al.*, 2013; Lohbeck *et al.*, 2015).

6.3 Recommendations for future research

Besides the research plans mentioned in the previous subsection, my PhD research supports the need for further studies on several topics.

There is a general need to increase research on the ecology of tropical dry forests to better understand how they differ from other tropical forest biomes (Sanchez-Azofeifa *et al.*, 2005; Quesada *et al.*, 2009). A focus on less studied regions (Africa, Asia and the Pacific area) is especially important. Moreover, standardised protocols and multi-site research projects (Quesada *et al.*, 2009) would be especially valuable in enabling the effect of regional-scale factors (such as climate, and the plant and animal species pool) to be tested.

As mentioned in section 5.2, several factors likely to affect successional trajectories need to be tested further: landscape factors, past and present land uses and remnant vegetation. Multi-disciplinary approaches using field-based ecological studies, remote sensing and social science would be particularly interesting (Sanchez-Azofeifa *et al.*, 2005; Castillo-Nunez *et al.*, 2011; Chazdon, 2014).

More studies assessing the relative contributions of deterministic and stochastic components in succession, such as the study of Norden *et al.* (2015) showing their equal contribution to successional dynamics in neotropical forests, are needed to inform theoretical models of succession. Vellend *et al.* (2014) critically reviewed appropriate methods to do so, such as the use of null models in observational studies or experimental approaches manipulating the order of colonisation of different species during succession, though the latter approach would be difficult for long-lived organisms such as trees.

The importance of intraspecific trait variation is increasingly acknowledged. As mentioned in the previous section, it is now important to assess the processes (environmental drivers and ontogeny) driving this variation (Lepš *et al.*, 2011; Violle *et al.*, 2012; Spasojevic *et al.*, 2014), as well as the spatial scales at which they affect community assembly (Siefert *et al.*, 2015; Spasojevic *et al.*, 2016). Such studies will help to refine sampling protocols to study the changes in community-level trait values with environmental gradients. Lastly, distinguishing the contributions of genetic variation and phenotypic plasticity to intraspecific variation in functional trait values is important, not only for ecological theory but also for application to ecological restoration. A strong contribution of genetic variation would emphasise the importance of considering the provenance of propagules used for direct seeding or planting. On the other hand, if phenotypic plasticity is the main mechanism causing intraspecific variation, using species with a high plasticity could be valuable to mitigate unexpected changes in environmental conditions that could result from local disturbance or global climate change. To assess the relative importance of genetic variation and phenotypic plasticity, experimental studies are needed, including the use of long-established methods such as common garden and transplant experiments.

7 Conclusion

Tropical dry forests are fascinating environments, especially for the variety of their colours and ambiance changing with the seasons. They are also endangered ecosystems that have been threatened by human activities for a very long time. The increasing attention that they are receiving from scientists, managers and the general public is a positive sign for their future.

In the last two or three decades, studies of the ecology of tropical dry forests have led to the recognition of their specific characteristics and the need to move beyond the extrapolation to these forests of ecological models that have been developed in tropical moist and temperate forests. They have also shown heterogeneity among tropical dry forests. Successional trajectories, because of the complexity of the multiple interacting factors influencing them, still appear to be very context-dependent. Further research is therefore needed to identify the relative importance of these factors, especially regarding the role of the landscape and the legacies of past land uses, and to get a more unified understanding of the driving forces of succession across tropical dry forests.

Awareness-raising and involvement of the general public, and especially of the population living in surrounding areas, is of the utmost importance for the conservation and restoration of tropical dry forests. Initiatives such as the educational and ecotourism programs led by the *Área de Conservación de Guanacaste* are playing a great role in demonstrating the richness and fragility of these forests and encouraging the local population and visitors to contribute to their protection and restoration.

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Appendices

Appendix 1. Characteristics of the species tested in the study of seed fate.

Species	Family	Seed mass (g)[1]	Seed size (mm^3)[1]	Presence of hard seed coat[1]	Dispersal mode[2]	Successional status[3]
Astronium graveolens	Anacardiaceae	0.013	13.6	no	anemochorous	late succession
Cochlospermum vitifolium	Bixaceae	0.023	25.4	yes	anemochorous	early succession
Dalbergia retusa	Leguminoseae	0.060	63.5	no	anemochorous	generalist
Hymenaea courbaril	Leguminoseae	3.205	2444.1	yes	zoochorous	mid to late succession
Simarouba amara	Simaroubaceae	0.855	1262.4	yes	zoochorous	mid to late succession
Stemmadenia obovata	Apocynaceae	0.060	69.7	no	zoochorous	mid to late succession
Thouinidium decandrum	Sapindaceae	0.062	181.6	no	anemochorous	generalist

1. Data from Géraldine Derroire (unpublished), average of the measurement of 25 seeds.
2. Data provided by Powers and Tiffin (2010) supplemented by information obtained from local experts (Roberto Espinoza and Daniel Perez Avilez).
3. Data provided by Leland Werden and Jennifer Powers (unpublished) based on the analysis of species abundance in a chronosequence of 84 plots in the *Área de Conservación de Guanacaste* and in Palo Verde (Costa Rica).

Appendix 2. Characteristics of the three sites used in the study of seed fate.

	Sites		
	Open site	Young secondary forest	Intermediate-aged secondary forest
Successional age (years)	0	~ 15	~ 30
Proportion deciduous (%)[1]	NA	72.7 ^{a}	56.7 ^{a}
Proportion zoochorous (%)[1]	NA	37.4 ^{a}	70.9 ^{a}
Canopy height (m)	NA	15.2 ^{a}	17.8 ^{a}
Canopy openness (%)			
dry season	100 ^{a}	22 ^{b}	12 ^{c}
wet season	100 ^{a}	10 ^{b}	8 ^{c}
Air temperature (°C)			
dry season	29.4 ^{a}	28.1 ^{b}	26.7 ^{c}
wet season	26.7 ^{a}	25.2 ^{b}	24.5 ^{c}
Red : Far red ratio	0.56 ^{a}	0.38 ^{b}	0.77 ^{a}

1. Proportion of the basal area of all trees with DBH ≥ 1 cm measured in a circular plot of 10 m radius centred on the seed plot.

All data from Géraldine Derroire (unpublished).

Letters indicate significantly different values (t-test, ANOVA or Kruskal-Wallis test and post-hoc test).

Appendix 3. Effect of litter treatment and site on microclimatic conditions in the study of seed fate.

	Effect of litter treatment	Effect of site[1]	Effect of interaction site * litter treatment
Soil temperature[2]	**$p = 0.031$** litter < no litter	**$p < 0.001$** inter. < young < open	$p = 0.898$
Soil moisture[2]	$p = 0.459$	$p = 0.066$	$p = 0.331$
Air humidity[2]	**$p = 0.017$** no litter < litter	**$p < 0.001$** open < young < inter.	$p = 0.846$
Litter depth	**$p < 0.001$** no litter < litter[3]	**$p < 0.001$** open[4] < young < inter.	**$p < 0.001$**

1. *Inter.* stands for intermediate-aged forest, *young* for young forest and *open* for open site.
2. Measured during the wet season.
3. This is a direct consequence of the litter removal.
4. In the open site, the litter is not woody plant leaf litter but rather dry material from the growth of herbaceous plants (thatch) in the previous year.

All data from Géraldine Derroire (unpublished).

p-values were obtained from two-way ANOVAs, results that are significant at $p < 0.05$ are shown in bold.

Publications

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REVIEW

The Effects of Established Trees on Woody Regeneration during Secondary Succession in Tropical Dry Forests

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ABSTRACT

Understanding the mechanisms controlling secondary succession in tropical dry forests is important for the conservation and restoration of this highly threatened biome. Canopy-forming trees in tropical forests strongly influence later stages of succession through their effect on woody plant regeneration. In dry forests, this may be complex given the seasonal interplay of water and light limitations. We reviewed observational and experimental studies to assess (1) the relative importance of positive and negative effects of established trees on regeneration; (2) the mechanisms underlying these effects; and (3) to test the 'stress gradient hypothesis' in successional tropical dry forests. The effects of established trees on seed dispersal, seed survival, and seed germination—either through direct changes to moisture and temperature regimes or mediated by seed dispersers and predators—are mainly positive. The balance between positive and negative effects on seedling establishment is more complex and depends on the season and leaf phenology of both trees and seedlings. Seedling survival is generally enhanced by established trees mitigating dry conditions. Established trees have counteracting effects on water and light availability that influence seedling growth. The probability of a positive effect of established trees on seedling survival decreases with increased rainfall, which supports the stress gradient hypothesis. Priorities for future research are experiments to test for facilitation and competition and their underlying mechanisms, long-term studies evaluating how these effects change with ontogeny, and studies focusing on the species-specificity of interactions.

Key words: competition; facilitation; germination; seed dispersal; seedling establishment; shade effects; stress gradient hypothesis; water limitation.

Plant–plant interactions are important for structuring plant populations and communities (Bertness & Callaway 1994) and can influence ecological processes and patterns up to the landscape scale (Bruno *et al.* 2003). These interactions are influenced by the direct or indirect ways that one plant makes the abiotic and biotic environment more favorable (*i.e.,* facilitation) or unfavorable (*i.e.,* competition) for another (Callaway 2007, Brooker *et al.* 2008). Following major disturbance the interactions between the first established plants and subsequent ones are critical for understanding of succession (Connell & Slatyer 1977, Brooker *et al.* 2008), but succession is a complex process also involving other factors that act across scales, such as land use and disturbance history, seed dispersal limitation, soil properties, plant–animal interactions (Chazdon 2003, Hobbs *et al.* 2007, Holl 2012), and stochastic events (Young *et al.* 2005).

Tropical dry forests (TDF) have undergone widespread conversion into agriculture (Sanchez-Azofeifa & Portillo-Quintero 2011) and are one of the Earth's most threatened ecosystems (Janzen 1988, Miles *et al.* 2006). However, they have been far less studied than tropical moist and temperate forests (Quesada *et al.* 2009). Many TDF have regrown after the abandonment of agriculture and are undergoing secondary succession driven by remnant organisms or their propagules (Chazdon 2003). A better understanding of the ecology of TDF secondary succession is needed to inform the design of science-based restoration practices (Vieira & Scariot 2006b), as well as to test ecological theories and models.

The stress gradient hypothesis predicts that facilitation is more important when environmental conditions are particularly harsh (Bertness & Callaway 1994, Callaway 1995, Callaway & Walker 1997). Tropical dry forests are highly seasonal environments, meaning they are also seasonally stressful ones. During the rainy season water is rarely limiting and instead light becomes the main factor limiting regeneration. Moreover, micro-climatic conditions change during early secondary succession in TDF because of the rapid increase in stem density, cover, and aboveground biomass (Kennard 2002, Lebrija-Trejos *et al.* 2010, Maza-Villalobos *et al.* 2011, Becknell *et al.* 2012). Shade of established trees can increase soil moisture by reducing air and soil temperature and increasing relative humidity (Lebrija-Trejos *et al.* 2011), which lowers transpiration from tree seedlings and other subcanopy plants. Litter from established trees also reduces evaporation from the soil surface, and its decomposition enhances soil organic matter that increases water retention in the soil (Sayer 2006, Xiong *et al.* 2008). However, these effects are strongly counteracted by the transpiration of canopy trees, which acts as the major sink for soil moisture in forests (Lebrija-Trejos *et al.*

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2011). In contrast, if the roots of canopy trees take up water from deeper in the soil (hydraulic lift), this can increase water availability to shallow-rooted seedlings (Callaway 2007). The balance between positive and negative interactions in successional TDF is therefore complex and dependent on the life stage of the individuals involved, their physiology, indirect interactions via other organisms, and the intensity of abiotic constraints (Callaway & Walker 1997).

Our objective is to understand the mechanisms by which the first generation of trees regenerating in successional TDF (referred to hereafter as 'established trees') influences the regeneration of woody plants from the local species pool, and therefore secondary succession. We focus on the early and critical stages of the process of regeneration (*sensu* Grubb 1977)—seed dispersal, survival of seeds, germination, and seedling establishment (Poorter 2007) to answer the following questions. (1) What is the relative importance of positive and negative effects of established trees on woody plant regeneration? We expect that overall the effects of established trees are positive, that is, they ameliorate the stressful environmental conditions in TDF. We also expect that the effects of established trees vary across the stages of regeneration because of the changing requirements of young plants. (2) What are the mechanisms by which established trees influence regeneration? We expect that the primary direct mechanism by which established trees influence regeneration is by providing cover that mitigates harsh micro-climatic conditions. However, we predict that this positive effect is less important for seedling growth because growth occurs mainly during the wet season when availability of water is generally not limited (Rincón & Huante 1993). We also expect indirect effects of established trees mediated by animals, especially for the seed dispersal stage. (3) Finally, do previously published studies of regeneration in TDF support the stress gradient hypothesis? We expected the positive effect of established trees to be more important in sites with a low mean annual rainfall (MAR) where water availability is more limited.

METHODS

Selection of studies for review.—In April 2012, we searched the *Web of Science* and *Science Direct* databases using the following combination of keywords (succession* OR secondary) AND tropical AND dry AND forest* AND (competition OR facilitation OR nurse* OR restoration). We supplemented this search with a small number of additional studies found via the references cited in the included studies. The search was updated regularly until June 2015 using the same search strategy.

Selection criteria.—We selected for inclusion in our review all studies meeting the following two criteria. First, studies had to be conducted in TDF, defined as forests with a mean annual rainfall (MAR) of 500–2000 mm and mean annual temperature (MAT) >17°C (Holdridge 1967, Becknell *et al.* 2012) with at least 3 mo of severe drought (rainfall <100 mm) (Sanchez-Azofeifa *et al.* 2005). This includes forests with varying degrees of deciduousness (Vieira & Scariot 2006b). Second, studies had to focus on forests undergoing secondary succession. We excluded from our review studies of succession on sites where the disturbance was such that soil was initially lacking (*e.g.*, due to mining or volcanic eruption), because processes occurring during primary succession differ from those occurring during secondary succession (Chazdon 2003). Moreover, secondary succession is far more common than primary succession in the TDF biome because of the attractiveness of TDF for human activities and particularly agriculture (Aronson *et al.* 2005). Alternatively, studies were selected for the inclusion that tested the effect of established trees by comparing them with open areas or by comparing the different types of tree cover, or manipulated environmental conditions (*e.g.*, by shading or additional watering) in a natural or controlled environment (*e.g.*, shadehouse).

Data collection.—We sorted the selected studies by the regeneration stage they investigated: seed dispersal, seed survival, seed germination, and seedling establishment. We use the term seed to refer to the dispersal unit, sometimes called a propagule or dispersule, because for the majority of species considered, the unit is a seed. However, in some species the unit also included part or all of the fruit. In addition, while the seedling establishment phase starts with seed germination, definitions of the end of this phase are often quite arbitrary (Grubb 1977). Some definitions, mainly for forest vegetation surveys, propose a maximum seedling size, generally 1 or 1.3 m (Newton 2007). However, the time needed to reach this size can vary greatly depending on the species and environmental conditions, which is why most studies of seedling establishment are carried out for a fixed time period after germination. For the studies we reviewed that reported this time period the average was 20 mo (range: 2–50 mo). We therefore consider the seedling establishment phase as approximately the first 2 yr of the life of a tree, recognizing it can extend up to 4 yr. Throughout the text we report seedling survival and growth for the duration of the seedling establishment phase considered by the original studies.

To evaluate the relative importance of positive and negative effects of established trees on each woody plant regeneration stage, we searched the selected studies for results comparing each regeneration stage at (1) different stages of succession or (2) between areas with established trees and open areas. These comparisons summarize the net outcome of positive and negative effects of established trees on subsequently establishing ones; for this reason, we favor the use of the terms 'net positive effects' or 'net negative effects' rather than facilitation or competition.

To understand which mechanisms underlie the effect of established trees on woody plant regeneration we used studies testing the correlation between the outcome of the regeneration stage under consideration and the environmental factors being manipulated or compared. For example, to test the effect of shade provided by established trees on seedling growth, we used studies testing for correlations between seedling growth and the amount of shade. When we found no such studies, we searched the discussion of the selected studies for possible hypotheses regarding the mechanisms.

Finally, data on MAR reported in studies was used to test if the net effect of established trees depends on MAR.

DATA ANALYSIS.—Although we initially hoped to conduct a meta-analysis of effect sizes for each of the research questions (Koricheva & Gurevitch 2014), we were unable to because of the low number of studies for some questions, the heterogeneous measures of plant responses and treatments applied, and because few of the studies reported any measure of variance in their results. To test the stress gradient hypothesis in the context of regeneration in TDF secondary succession, we analyzed the net outcome of the effect of established trees on seedlings with logistic regressions (binomial generalized linear models with logit link function), using both survival and growth as dependent variables. To test for net positive effects, we scored as '1' for the studies that show a net positive effect and '0' for the studies that show a non-significant or negative effect. In contrast, to test for net negative effects, we scored '1' for the studies that show a net negative effect and '0' for those that report a non-significant or positive effect. We then used these values to fit four models (for net positive and negative effects, and for survival and growth) against the MAR using the R statistical programming language (R core team 2013). The low number of studies found for the other stages of regeneration did not allow such analysis.

RESULTS

SELECTED STUDIES.—The first search yielded 206 studies, of which 29 met our criteria (Table 1). The numbers of studies for each methodological approach were quite similar (Table 1). For the studies of forests that were undergoing secondary succession, the previous land use was generally agriculture (cultivation or pasture) and the timing varied from immediately after abandonment to several decades later (Table 2). Of studies meeting our criteria, 20 were carried out in the Neotropics (69% of all included studies), mainly in Mexico, Brazil, and Costa Rica. Four studies were carried out in Asia (14%), three in the Pacific (Hawaii, 10%), and two in Africa (Ethiopia, 7%).

EVIDENCE OF POSITIVE AND NEGATIVE INTERACTIONS AND THE UNDERLYING MECHANISMS.—The numbers of studies on seed dispersal, seed survival, and seed germination were very low (five, three, and four, respectively). There were 21 studies on the seedling establishment stage (Table 1). Ten studies reported the overall net outcome of established trees on seedlings (Table 3). Eight experimental studies artificially controlled light and water availability (Table 4). A summary of the positive and negative effects of established trees on regeneration and the mechanisms influencing each stage of regeneration is presented in Fig. 1.

STRESS-GRADIENT HYPOTHESIS.—Due to low number of studies, we were only able to test the stress-gradient hypothesis with studies of seedling establishment. We found that the probability of a net

TABLE 1. *Selected studies. The total number of studies is 29 and the number of studies per regeneration stage and/or methodological approach is indicated in bold in the table. Some studies considered more than one regeneration stage and/or used more than one approach.*

	Regeneration stage			
Methodological approach	Seed dispersal, **5 studies**	Seed survival, **3 studies**	Germination, **4 studies**	Seedling establishment, **21 studies**
In secondary successional forests, **13 studies**	Ferguson *et al.* (2003), Opler *et al.* (1980), Teegalapalli *et al.* (2010), Wydhayagarn *et al.* (2009), **4 studies**	Hammond (1995), **1 study**	Ray and Brown (1995), **1 study**	Cabin *et al.* (2002a), Cabin *et al.* (2002b), Gerhardt (1996), Gerhardt (1998), Gonzâlez-Rivas *et al.* (2009), Hammond (1995), Ray and Brown (1995), Santiago-Garcia *et al.* (2008), Thaxton *et al.* (2012), **9 studies**
Comparison of open areas and established tree cover or of different tree cover, **16 studies**	Teegalapalli *et al.* (2010), Wydhayagarn *et al.* (2009), Zelikova and Breed (2008), **3 studies**	Vieira and Scariot (2006a), Wassie *et al.* (2010), **2 studies**	Hardwick *et al.* (1997), **1 study**	Cabin *et al.* (2002a), Castro-Marin *et al.* (2011), Gonzâlez-Rivas *et al.* (2009), Hoffmann (2000), Marod *et al.* (2004), McLaren and McDonald (2003b), Santiago-Garcia *et al.* (2008), Teketay (1997), Vieira *et al.* (2006), Wolfe and Van Bloem (2012), **10 studies**
Experimental manipulation of environmental conditions **12 studies**	**0 study**	**0 study**	Blain and Kellman (1991), Hardwick *et al.* (1997), McLaren and McDonald (2003a), Ray and Brown (1995), **4 studies**	Badano *et al.* (2011), Blain and Kellman (1991), Cabin *et al.* (2002b), Gerhardt (1996), Gerhardt (1998), Marod *et al.* (2004), McLaren and McDonald (2003a), Ray and Brown (1995), Rincón and Huante (1993), Thaxton *et al.* (2012), Vieira *et al.* (2008), **11 studies**

positive effect of established trees on survival of seedlings decreased with increasing rainfall (χ^2 test $P = 0.008$, $R^2 = 0.43$), whereas the probability of a net negative effect increases with rainfall ($P = 0.009$, $R^2 = 0.56$) (Fig. 2). In contrast, there was no evidence of a correlation between net positive effect ($P = 0.853$) or net negative effect ($P = 0.862$) on seedling growth and MAR.

TABLE 2. *Location and site history of the reviewed studies of forests that were undergoing secondary succession. Studies that just compared open areas and areas with established trees, and experimental studies carried out in controlled environments are not included in this table.*

Reference	Country	Past land use	Time since the beginning of secondary succession (abandonment of past land use) (yr)
Cabin *et al.* (2002a)	Hawaii	Degradation by cattle and feral goats	42
Cabin *et al.* (2002b)	Hawaii	Human disturbance	1–2
Ferguson *et al.* (2003)	Guatemala	Agriculture (agroforestry, swidden cultivation, pasture, intensive monoculture)	0–4
Gerhardt (1996)	Costa Rica	Pasture	25
Gerhardt (1998)	Costa Rica	Pasture	25
Gonzâlez-Rivas *et al.* (2009)	Nicaragua	Agricultural crops	4, 9, 14
Hammond (1995)	Mexico	Shifting agriculture	2, 4, 10, 30
Ray and Brown (1995)	Virgin Islands	Grazing	35
Santiago-Garcia *et al.* (2008)	Puerto Rico	Pasture	0
Teegalapalli *et al.* (2010)	India	Rice cultivation	4
Thaxton *et al.* (2012)	Hawaii	Degradation by ungulates and fire	>10
Wydhayagarn *et al.* (2009)	Thailand	Agricultural crops	8 (active restoration)

TABLE 3. *Main results of studies on effects of established trees on seedlings in tropical dry forests. + indicates a positive effect of established trees on seedlings, − indicates a negative effect and 0 indicates an absence of significant effect. Several types of effect are indicated as +/0 or 0/−, meaning that the effect differs between seedling species. Mean annual rainfalls are those given in the source papers. When shown, the standard error reflects the variation between years. The number of dry months can be given as a range* (e.g., *4 to 5). When there are two dry seasons, the length of both is given* (e.g., *5 and 3). The number of studied seedling species distinguishes those that are experimentally seeded or planted, or naturally regenerated ("natural").*

Reference	Community leaf phenology	Mean annual rainfall (mm)	Number of dry months	Number of studied seedling species	Treatments	Net effect of established tree on survival	Net effect of established tree on growth
Cabin *et al.* (2002a)	No data	500	Irregular	6 (seeded)	Closed canopy, open area	+	No data
McLaren and McDonald (2003b)	No data	780	4 to 5	64 (natural)	Clearcut, 50% cut, uncut	+	−
Santiago-Garcia *et al.* (2008)	No data	860	4 and 2	24 (planted)	Closed canopy, open area	+	+
Wolfe and Van Bloem (2012)	No data	860	4 and 2	14 (planted)	Forest, un-burnt, and burnt grass area	+	−
Teketay (1997)	Evergreen	1200	5 and 1	2 (natural) 3 (planted)	Closed canopy, open area	+/0	0/−
Vieira *et al.* (2006)	Deciduous	1236 ± 50	6	7 (planted)	Closed canopy, open area	+	−
Gonzâlez-Rivas *et al.* (2009)	Deciduous	1431 ± 369	5	2 (survival) 1 (growth) (all planted)	Closed canopy, partially open, open area	−	−
Castro-Marin *et al.* (2011)	Deciduous	1431 ± 369	5	3 (survival) 1 (growth) (all planted)	Closed canopy, partially open, open area	−	−
Hoffmann (2000)	No data	1480	5	3 (forest species, planted)	Dense canopy, intermediate, open area	+/0	+
Marod *et al.* (2004)	Deciduous	1546	5	6 (planted)	Closed canopy, open area	−	−

TABLE 4. *Main results of studies on the effects of light and water factors on seedling establishment in tropical dry forests. + indicates a positive effect of shading/watering on seedlings, − a negative effect and 0 an absence of significant effect. +/0, +/− and 0/− indicate that results vary between seedling species. N stands for nursery, GC for growth chamber, GH for greenhouse, F for field, Natural for naturally regenerating, NT for not tested, S for shading, NS for no shading, W for watering, and NW for no watering.*

	Cabin *et al.* (2002b)	Thaxton *et al.* (2012)	Rincón and Huante (1993)	Badano *et al.* (2011)	McLaren and McDonald (2003a)	Ray and Brown (1995)	Vieira *et al.* (2008)	Marod *et al.* (2004)
Experiment	F	F	GC	F	N	F	GH	F
Location	Hawaii	Hawaii	Mexico	Mexico	Jamaica	Virgin Islands	Brazil	Thailand
Mean annual rainfall (mm)	500	500–750	748	750–900	780	1140	1236	1546
Number of dry months	Highly variable	Not distinctly seasonal	8	8	4–5	4	6	5
Number of studied species	12 and natural	11	5	2	4	10	8	6
Water treatment	NT	Additional, ambient	NT	NT	Regular W, NW	NT	NT	W during dry season, NW
Artificial shading (% of full sunlight)	NS, S (50%)	NS, S (60%)	As in medium size gap, as under canopy	NS, S (20%)	NS (86%), partial S (37%), heavy S (6%)	NS, S (25%)	NS (72%), partial S (40%), heavy S (10%)	NT
Effect of supplementary water								
Survival	NT	+	NT	NT	+	NT	NT	+/0
Growth								
Diameter	NT	NT	NT	NT	+	NT	NT	+/0
Height	NT	0	NT	NT	+	NT	NT	0
Effect of shading								
Survival	+/0	+	NT	+	+	+	+	NT
Growth								
Diameter	NT	NT	NT	NT	+ (Partial S), − (Heavy S)	NT	+/−	NT
Height	NT	+	NT	NT	+	0	NT	NT
Biomass	NT	NT	−	NT	NT	0/−	+/−	NT
Effect of interaction between supplementary water and shading								
Survival	NT	0	NT	NT	+	NT	NT	NT
Growth								
Diameter	NT	NT	NT	NT	0	NT	NT	NT
Height	NT	0	NT	NT	0	NT	NT	NT

DISCUSSION

EFFECTS OF ESTABLISHED TREES ON SEED DISPERSAL.—Areas with established trees have been shown to have enhanced seed rain when compared with open areas (Callaway 2007), and the results of studies conducted in TDF are consistent with this observation. However, we also found that this is highly dependent on the seed dispersal agent. For zoochorous seeds this effect is mediated by animal dispersers, mainly birds and bats, which are attracted by established trees that can provide perches or food (Vieira & Scariot 2006b) (Fig. 1). Studies of seedlings often show a high percentage of zoochorous species under tree canopies (Wydhayagarn *et al.* 2009), and chronosequence studies show an increase in the proportion of zoochorous species during secondary succession (Opler *et al.* 1980). Ferguson *et al.* (2003) also observed that the recruitment of fleshy-fruited individuals was higher when trees were present in the previous land use (agroforestry and swidden cultivation), and that it was positively correlated with the basal area of trees present at the start of succession. Features of trees responsible for attraction of dispersers are not well understood, however. It is probable that animal dispersers are attracted to particular tree species because of their flowers and fruits, branching structures, or sizes (Wydhayagarn *et al.* 2009). Zelikova and Breed (2008) also suggested that established trees can affect the dispersal of seeds by ants; they found that seeds of two fleshy-fruited species were removed less often in successional forests compared with open sites (~20% vs. ~65%), but that they were dispersed longer dis-

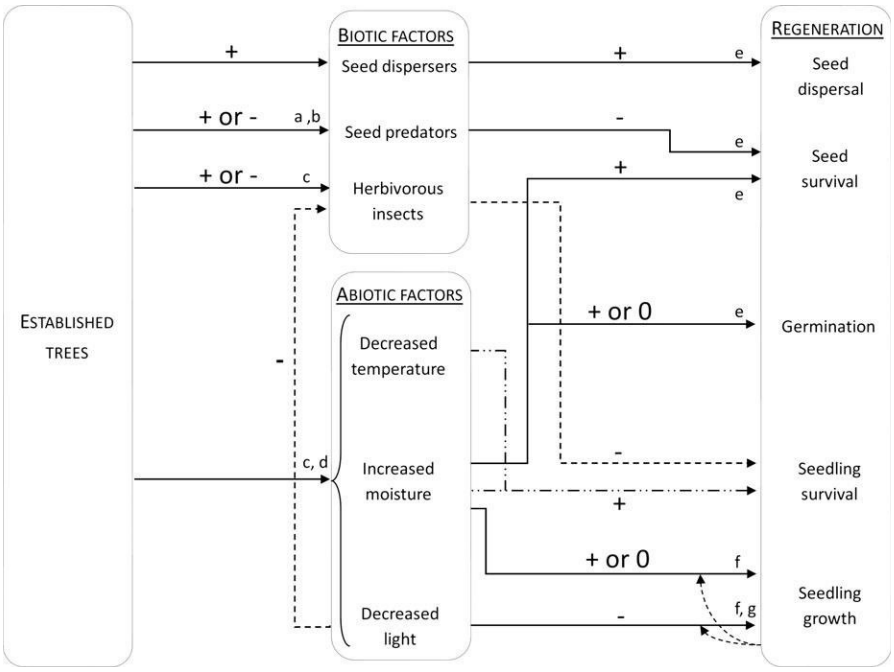

FIGURE 1. Mechanisms underlying the effect of trees that establish in the early stages of secondary succession on subsequent regeneration of woody plants in seasonally dry tropical forests. Each mechanism is shown by two arrows: one from the established trees' box to either the box of abiotic factors or the box of biotic factors and the other from the factors' box to the regeneration box. This figure synthesizes the main trends discussed in the review. The plus, minus, and zero symbols indicate positive, negative, and absence of effect, respectively. The different types of arrow are only used for the visual clarity of the figure. The letters on the arrows refer to the factors influencing the effect considered: (A) successional stage, (B) predator type, (C) leaf phenology of the established tree species, (D) density of canopy cover, (E) seed type, (F) regenerating species, and (G) intensity of shading.

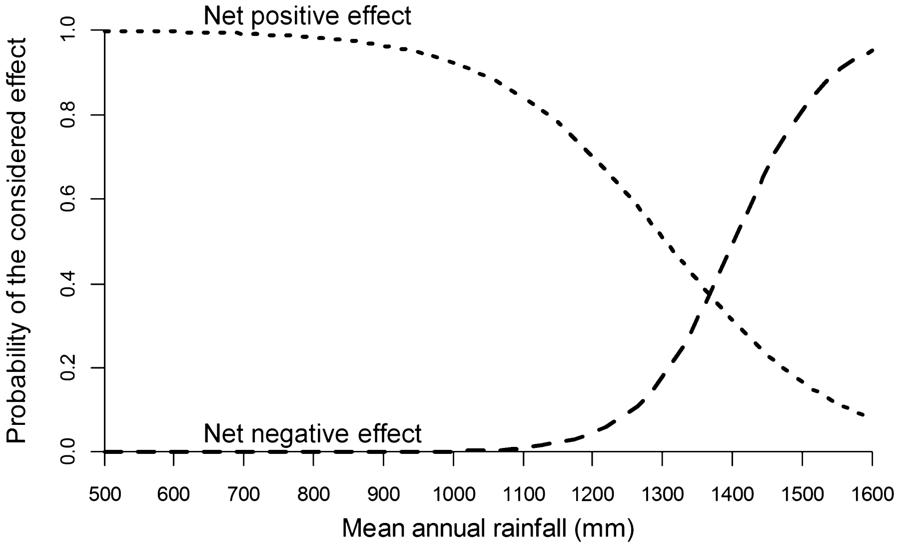

FIGURE 2. Probability of observing a net positive effect or a net negative effect of established trees on seedling survival in seasonally dry tropical forests as a function of the mean annual rainfall. Models fitted with logistic regressions: positive effect ($P = 0.008$, $R^2 = 0.43$), negative effect ($P = 0.009$, $R^2 = 0.56$)

tances (1.1 m vs. 0.5 m). However, more studies are needed to see if this is generally true.

In contrast, we found that the input rate of seeds of anemochorous woody plant species was mainly influenced by the distance to the source of seeds (Teegalapalli *et al.* 2010). Because they create turbulence in the laminar flow of wind, it has been argued that the crowns of trees can act as a seed trap for anemochorous species in many systems (Callaway 2007). To the best of our knowledge, however, this possibility has not been studied in successional TDF.

EFFECTS OF ESTABLISHED TREES ON POST-DISPERSAL SURVIVAL OF SEEDS.—Vieira and Scariot (2006a) found that seed desiccation appears to be more important in open areas than under tree canopies. This suggests a positive effect of tree canopy cover on seed survival via mitigation of conditions that desiccate seeds. However, species differ in the susceptibility of their seeds to desiccation under the dry conditions of early successional environments; Vieira and Scariot (2006a) showed that species with thin seed coats and high water content had a higher sensitivity to desiccation in open pasture than did other species.

The changes in seed predation and removal by animals in different successional stages are more complex (Fig. 1). Hammond (1995) found that seeds in old successional (>30 yr) and mature forest were less prone to predation, which he attributed to the thickness of the litter layer that protects seeds from rodents and other predators. However, Wassie *et al.* (2010) found some evidence of higher rates of seed predation by rodents under a closed canopy (~93%) than gaps (~87%), which they attributed to gap-avoidance by rodents. Vieira and Scariot (2006a) showed that differences in the patterns of seed predation during secondary succession depended on the type of seed. They attributed this to variation in the activity of different seed predators ranging from insects to large mammals in forests at different successional stages. More studies, especially if they measure micro-scale climatic conditions, are needed to disentangle these complex effects of established trees on seed desiccation and predation that depend on the interaction of type of seed, type of consumer, and successional stage.

EFFECTS OF ESTABLISHED TREES ON SEED GERMINATION.—Through the measurement of seed germination relative to natural seed rain, Hardwick *et al.* (1997) showed a higher germination rate under forest cover than under the cover of herbs and shrubs in post-agricultural successional vegetation in Thailand. For one species they documented 96 percent of germination in forest versus 1 percent at the edge of a clearing and 54 percent at the centre of a clearing; for another species germination in these habitats was 11, 8, and 7 percent (respectively). The values for the first species suggest that canopy cover might have a positive effect on seed germination (Fig. 1), which is consistent with the results of two of three studies carried out in controlled environments (Hardwick *et al.* 1997, McLaren & McDonald 2003a, but see Ray & Brown 1995). Supplementary watering also had a positive effect on germination in the experiment of McLaren and McDonald (2003a), but the results of Hardwick *et al.* (1997) were species-specific. Both studies also found an interaction of shading and watering treatments, at least for some of the tested species. McLaren and McDonald (2003a) observed that watering increased germination rate only for the unshaded treatments, which suggests that supplementary water is needed only under the desiccating environment of full sunlight. Moisture conditions therefore seem to be important in explaining the positive effect of established trees on seed germination of TDF species. However, more field studies are required to substantiate these effects, especially those monitoring seasonal variation in soil moisture under different forms of vegetation cover.

The response of seed germination to established trees is likely to differ between species. Of the three species that they tested, Hardwick *et al.* (1997) found that germination was most strongly promoted by shade or by additional watering in the largest-seeded species. Shading also promoted germination of the two small-seeded species, but additional watering benefited germination only for one of the two. Tests of a greater number of species are needed to establish relationships with seed traits such as seed moisture content, seed size, and presence of a hard coat.

EFFECTS OF ESTABLISHED TREES ON SEEDLING ESTABLISHMENT.—A majority of studies reported a positive net effect of established trees on seedling survival for at least some of the seedling species studied (Teketay 1997, Hoffmann 2000, Cabin *et al.* 2002a, McLaren & McDonald 2003b, Vieira *et al.* 2006, Santiago-Garcia *et al.* 2008, Wolfe & Van Bloem 2012). However, some studies did report a net negative effect (Marod *et al.* 2004, González-Rivas *et al.* 2009, Castro-Marin *et al.* 2011). In contrast, for seedling growth the majority of studies reported a negative effect of established trees (but see Hoffmann 2000, Santiago-Garcia *et al.* 2008).

Established trees appear to influence seedling mortality by changing water availability (Fig. 1). Six experimental studies reported a positive effect of shading on TDF seedling survival (Ray & Brown 1995, Cabin *et al.* 2002b, McLaren & McDonald 2003a, Vieira *et al.* 2008, Badano *et al.* 2011, Thaxton *et al.* 2012), which Cabin *et al.* (2002b) attributed to mitigation of desiccating conditions. Moreover, the three studies that experimentally altered water availability all showed a positive impact of additional watering on seedling survival (McLaren & McDonald 2003a, Marod *et al.* 2004, Thaxton *et al.* 2012). Water shortage was put forward as the main cause of mortality during the TDF dry season (Lieberman & Li 1992, Gerhardt 1996, Cabin *et al.* 2002a, Marod *et al.* 2002, Vieira & Scariot 2006b). However, the effect of established trees on seedling survival mediated via water balance is relatively small in early stages of succession, when the canopy cover is still predominantly open (Hammond 1995). Regarding seedling growth, the effect of water availability differs among studies (Table 4). This effect may depend on the soil type, in particular its texture and plant-available water capacity (McLaren & McDonald 2003a, Marod *et al.* 2004). An experiment in which root competition was eliminated with trenches showed a negative effect of established trees belowground, both on survival and growth of seedlings (Gerhardt 1996). Changes in water availability can affect seedling resource allocation (Blain & Kellman 1991), which can subsequently affect rates of water uptake (through allocation to root growth) and photosynthesis (through shoot allocation) and therefore modify the drought tolerance and growth of seedlings.

Reduction in light availability by established trees can have a negative effect on seedling growth (Rincón & Huante 1993, McLaren & McDonald 2003a, Fig. 1). However, Badano *et al.* (2011) found that shading improved the physiological performance of seedlings, associated with reduction in leaf temperature. Moreover, shade can have a different effect on the growth of different parts of the plant: McLaren and McDonald (2003a) found that heavy shading enhanced growth in height while reducing growth in diameter and Rincón and Huante (1993) found that shading induced a higher allocation of biomass to leaves. These results suggest that shade causes an allocation of resources toward growth that can increase photosynthesis in the subcanopy environment.

Our review suggests that the positive effect of established trees on seedling survival is predominantly mediated by moisture regime during the dry season and that the negative effect of trees on seedling growth is via limitation of light during the wet season (Cabin *et al.* 2002a, McLaren & McDonald 2003b, Vieira & Scariot 2006b, Wolfe & Van Bloem 2012). However, these effects are not independent, and physiological response of seedlings to one environmental condition may alter the effect of another. Rincón and Huante (1993) found that a higher light level induced a higher allocation of biomass to roots, which could enable a higher rate of water uptake and thus a reduction in mortality rate during the subsequent dry season.

The capacity of established trees to cast shade during the dry season depends on their leaf phenology (evergreen or deciduous). Because deciduous trees cast little shade during the dry season, the local openness of the canopy, and hence microclimatic stress, increases with the proportion of deciduous trees. We hypothesize that the established trees in these forests would have too little or no positive effect on seedlings during the dry season to counterbalance a negative effect during the wet season (Vieira *et al.* 2006). Of the four field studies carried out in deciduous forests, three showed an overall negative effect of established trees on seedling survival (Table 3). Moreover, experimental manipulation of aboveground effects by thinning trees (Gerhardt 1996) showed that in deciduous forest the dominant aboveground effect is negative. In contrast, in semi-evergreen forest that retains some foliage during the dry season the net aboveground effect varied among the regenerating species. Leaf phenology of seedlings is likely to explain their species-specific response to the effect of established trees; deciduous species, for which growth is limited to the wet season, may be more sensitive than evergreen species to the negative effect of shading during this season (Ray & Brown 1995). In contrast, evergreen and semi-deciduous species may be more sensitive to water loss by transpiration during the dry season than the deciduous species, as supported by Marod *et al.* (2004).

While research in TDF mainly focuses on effects mediated by light and moisture, there is also the potential for established trees to influence seedlings via competition for soil nutrients (Casper & Jackson 1997, Coomes & Grubb 2000) or increased nutrient availability to seedlings from litter decomposition (Callaway 2007, Berg & McClaugherty 2008, Cornwell *et al.* 2008, Fig. 1). Established trees could also have indirect effects on seedlings via insect herbivores (Fig. 1). Using a factorial experimental design that controlled above- and belowground interactions, Gerhardt (1998) found that the effects on seedlings of both were positive. She attributed the belowground effect to root competition, which could decrease the nutritional value of seedling leaves and therefore their palatability and susceptibility to herbivory. She attributed the aboveground effect to reduced light levels impeding insect activity (see also Badano *et al.* 2011). Nevertheless, the effects of herbivory on seedlings under canopy shade may be greater than in higher light levels; the consequences of reduced photosynthetic activity from lost leaf area are greater when photosynthesis is already limited at low light levels (Gerhardt 1998).

STRESS GRADIENT HYPOTHESIS.—We found that there is evidence in support of the stress gradient hypothesis for seedling survival but not for seedling growth. For survival, the switching point from a higher probability of positive to negative effects of established trees with increasing MAR appears to occur at around 1400 mm (Fig. 2). This MAR threshold is similar to that found by McDonald *et al.* (2010) for a shift in TDF to dominance by sexual instead of vegetative reproduction.

METHODOLOGICAL LIMITATIONS AND PRIORITIES FOR FUTURE RESEARCH.—The studies reviewed used a wide range of approaches. However, this diversity of methodological approaches can make it difficult to draw generalizations across studies. This issue, together with the low number of studies and the rarity with which they reported any measure of the variance of their results, prevents the use of meta-analytical techniques (Koricheva & Gurevitch 2014). Nevertheless, our review does elucidate trends, identify gaps in current knowledge, and suggest future research directions. We identified five components of the interactions between established trees and subsequent regeneration during secondary succession that we suggest are the main priorities for future research. (1) There is a need for more studies of root interactions and other belowground processes—either direct or mediated by mycorrhizal symbionts—and their impact on seedlings' capacity to acquire water and nutrients (Coomes & Grubb 2000). (2) More research should focus on indirect interactions mediated by biotic agents such as seed dispersers/predators, herbivorous insects, symbionts, or shared competitors, especially for the seedling establishment phase (Callaway 2007). (3) Factorial experiments in the field as well as in controlled environments are needed to distinguish between the effect of shading on photosynthesis through modification of irradiance and the effect on desiccation through modification of temperature and moisture of air and soil. (4) There is a need for long-term studies in a broader diversity of sites—most of the studies reviewed were conducted in the Neotropics—on how the interactions between established trees and seedlings change as the latter develop into saplings and adults (Gomez-Aparicio *et al.* 2004, Young *et al.* 2005, Callaway 2007). (5) Research on plant functional traits may help understanding of the species-specificity of the reviewed interactions. A focus on leaf phenological traits in both established trees and seedlings is particularly needed as leaf phenology influences aboveground microclimate and soil conditions through its effect on timing of water uptake and litter input (Hasselquist *et al.* 2010). Seed traits, especially seed size, moisture and nutrient content, and the presence of a hard coat, as well as traits related to the acquisition and use of resources, for example, allocation of biomass, dry matter content, and shoot and root architecture, should also be considered. Using a functional trait approach would be especially interesting to determine if there is a trade-off in drought and shade tolerance of seedlings among species, or if there is a dichotomy between resource conservative strategies (of species able to tolerate low availability of both light and water) and resource acquisitive strategies (for species that show higher growth rate but require greater availability of both light and water resources) (Wright *et al.* 2004). While some of the reviewed studies that compared evergreen and deciduous species in TDF support the trade-off hypothesis (Ray & Brown 1995, Marod *et al.* 2004), they studied too few species to allow extrapolation of this finding.

In seasonal TDF, direct or indirect interactions between established trees and woody plants regenerating below their canopy are important at every stage of the regeneration process. The positive effects of established trees at early stages of regeneration support the importance of facilitation during secondary succession. However, during subsequent stages of regeneration as seedlings establish and grow, the effects become more complex and dependent on seasonality of rainfall and on species. Nevertheless, the effect of established trees on seedling survival shifts from positive to negative when MAR increases, in accord with the stress gradient hypothesis. Overall, the effect of established trees on regeneration during secondary succession in TDF remains poorly understood and a fruitful area for further research.

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Paper II

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Resilience of tropical dry forests – a meta-analysis of changes in species diversity and composition during secondary succession

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Assessing the recovery of species diversity and composition after major disturbance is key to understanding the resilience of tropical forests through successional processes, and its importance for biodiversity conservation. Despite the specific abiotic environment and ecological processes of tropical dry forests, secondary succession has received less attention in this biome than others and changes in species diversity and composition have never been synthesised in a systematic and quantitative review. This study aims to assess in tropical dry forests 1) the directionality of change in species richness and evenness during secondary succession, 2) the convergence of species composition towards that of old-growth forest and 3) the importance of the previous land use, precipitation regime and water availability in influencing the direction and rate of change. We conducted meta-analyses of the rate of change in species richness, evenness and composition indices with succession in 13 tropical dry forest chronosequences. Species richness increased with succession, showing a gradual accumulation of species, as did Shannon evenness index. The similarity in species composition of successional forests with old-growth forests increased with succession, yet at a low rate. Tropical dry forests therefore do show resilience of species composition but it may never reach that of old-growth forests. We found no significant differences in rates of change between different previous land uses, precipitation regimes or water availability. Our results show high resilience of tropical dry forests in term of species richness but a slow recovery of species composition. They highlight the need for further research on secondary succession in this biome and better understanding of impacts of previous land-use and landscape-scale patterns.

Succession has been a major focus of plant community ecology for more than a century (McIntosh 1999), yet the processes underlying assembly of secondary forests continue to be actively researched (Norden et al. 2015). The early view of Clements (1916) (monoclimax hypothesis) and initial floristic composition model of Egler (1954) were further formalized by the three models of Connell and Slatyer (1977). These deterministic models are all based on the idea that tradeoffs between traits promote success in different stages of succession (Huston and Smith 1987). However, none of these models accounts for stochastic events or historical contingencies (Young et al. 2005). Lawton (1987) proposed a model of succession based only on random survival of established species and colonization by new species, paving the way for the neutral theory of community assembly (Hubbell 2001). Although deterministic niche-based and neutral models of succession have often been treated as mutually exclusive explanations for empirical patterns, a growing body of literature evidences the importance of the integration of the two (Chave 2004, Gravel et al. 2006, Tilman 2004). A major focus of research is now to assess the resilience of forests and the factors affecting it (Arroyo-Rodriguez et al. 2016, Norden et al. 2009). Resilience is defined here as the capacity and rate of recovery of the structure, composition and functioning that the forest had before disturbance (Chazdon and Arroyo 2013, Newton and Cantarello 2015). Niche-based deterministic processes promote a gradual return of the species previously present in old-growth forest and therefore lead to a good recovery of species composition, while neutral processes lead to more idiosyncratic trajectories of succession (Norden et al. 2009).

Complex interactions between intrinsic and extrinsic factors (Finegan 1984, Lebrija-Trejos et al. 2010) affect successional trajectories and therefore the resilience of forests. Within a given site, abiotic conditions (e.g. soil and climatic factors) affect plant regeneration. The nature and intensity of past land uses and current disturbances can lead to different rates of recovery of species composition (Kennard et al. 2002, Molina Colon and Lugo 2006). Remnant trees in abandoned pastures foster the establishment of young woody plants under their crown and influence the composition of these new plant assemblages (Derroire et al. 2016a, Guevara et al. 1986). At the larger scale of the landscape, remnant forests provide seeds that can be dispersed to adjacent successional forests (Chazdon 2014).

In the tropics, most studies of succession have been carried out in moist and wet forests. The resulting models are however not applicable to tropical dry forests (TDF) where there are different ecological processes and changes in functional composition with succession (Quesada et al. 2009, Lohbeck et al. 2013). In TDF, seasonal water limitations strongly determine ecological processes (Maass and Burgos 2011) while tropical wet forests are more limited by light availability and biotic interactions (Ewel 1977). Regeneration in TDF is characterized by the importance of vegetative reproduction, which can improve recovery of woody vegetation through resprouting, and by the high proportion of anemochorous species whose seeds can better colonise early successional sites (Vieira and Scariot 2006). During TDF succession, there is an extensive change in environmental conditions from hot and water-limited early stages towards more shaded later stages (Lebrija-Trejos et al. 2011), suggesting an important role of facilitative biotic interactions (Callaway and Walker 1997, Derroire et al. 2016b). However, the strength of the light gradient is lower in TDF than in wet forests due to smaller differences in light conditions between the early and late stages of succession (Ewel 1977, Letcher et al. 2015), suggesting a faster recovery of old-growth forest species. Furthermore, difference in precipitation regimes among TDF can affect successional processes. Becknell et al. (2012) synthesized the structural changes occurring during succession in TDF and showed that wetter sites reach a greater biomass than drier ones, suggesting steeper environmental gradients between early and late succession in wetter sites. McDonald et al. (2010) showed that the relative importance of resprouting and regeneration by seed changed with precipitation regimes, with resprouting being more important in drier sites. Derroire et al. (2016b) showed evidence that facilitation is more important in drier sites. These differences all suggest more differentiation between the species composition of early and late successional communities in TDF where precipitation is higher, in line with the findings of Letcher et al. (2015) that successional habitat specialisation is stronger for tropical wet forests than TDF.

Here we used meta-analysis of 13 chronosequences to assess the resilience capacity of TDF and the factors influencing it. The changes in biomass during succession have been quantitatively reviewed by Becknell et al. (2012) in TDF, Poorter et al. (2016) across Neotropical forests and Martin et al. (2013) across tropical forests. Martin et al. (2013) also reviewed changes in species richness and composition across tropical forests. Here we provide a new focus on the changes in species diversity (richness and evenness) and composition during secondary succession in TDF. We asked the following questions: 1) do species richness and evenness change in a directional way with succession and what are the direction and rate of change? If there are strong limitations to dispersal or if species arriving early in succession inhibit the arrival of other species, we expect limited or no changes in species richness, at least in the earlier stages. 2) How convergent are the changes in species composition with succession? In other words, does the composition of successional forests converge towards the composition of old-growth forests, indicating resilience, and how fast? Niche-based assembly should lead to an increasing compositional similarity between successional forests and old-growth forests, as environmental conditions change towards those of old-growth forests. On the other hand, inhibition of new species arrival by the early established vegetation would impede the increase in similarity. 3) Do the previous land use, precipitation regime and water availability affect the directionality and rate of change in species richness, evenness and composition during succession? We expect a difference between pasture and shifting cultivation land uses in their influence on subsequent succession because of their effects on the soil and remnant vegetation. Moreover, we expect the precipitation regime and water availability to influence the rates of change. The greater importance of resprouting and facilitation in drier forests predicts a faster accumulation of species. However, the greater range of environmental conditions and species successional habitat specialisation in wetter forests predicts a greater rate of change in species composition.

Methods

We have chosen a meta-analysis approach because it is a powerful and unbiased method to combine study results across multiple sites and test the effect of factors that are difficult to test with primary data (Koricheva and Gurevitch 2013), in our case previous land use, precipitation regime and water availability. Our methods follow the guidelines of Koricheva and Gurevitch (2014) and Woodcock et al. (2014) on methodology and reporting of systematic reviews and meta-analyses.

Data search and inclusion criteria

We searched Web of Science, Science Direct and JSTOR for studies of the composition of TDF during succession in April 2012. We used the following search string: (succession* OR secondary) AND tropical AND dry AND forest*. We complemented this search by screening the references cited by the publications we found, by searching books on TDF and asking colleagues for grey literature. We updated this search in June 2015 using Web of Science and Science Direct and the initial search string. A broader literature search on TDF found no additional relevant publications.

We used the following inclusion criteria to select relevant studies: 1) they considered TDF, defined as forests with a mean annual precipitation (MAP) between 500 and 2000 mm and mean annual temperature above 17°C (Becknell et al. 2012, Holdridge 1967) with at least three months of drought (precipitation $<$ 100 mm) (Sanchez-Azofeifa et al. 2005). 2) They studied natural succession. We excluded studies of forests where an active human intervention was conducted, such as restoration planting or fertilisation (Souza and Batista 2004). 3) They conducted an inventory of trees and shrubs in plots of different successional age (i.e. time since abandonment of the previous land use). They focused on adults, rather than on the soil seed bank, seedlings or saplings (Maza-Villalobos et al. 2011). 4) They provided information on previous land use. 5) They reported data from plots with at least three different values of successional age (to enable fitting of linear regression with successional age), using either a dynamic or a chronosequence approach. For the chronosequence approach, we checked that within datasets, plots were located on sites with the same climate, similar previous land use and no substantial known soil differences. We excluded studies with a different sampling design between the different successional ages (Larkin et al. 2012). 6) The youngest age of plots within a study was not more than 10 years, because case studies in TDF (Lebrija-Trejos et al. 2010) and global syntheses (Martin et al. 2013, Poorter et al. 2016) have shown rapid changes in the early stages of succession that we wanted to be able to assess across studies. 7) Because we calculated selected indices in order to assure comparability of studies, we needed raw data in the form of a floristic table of abundance of each species in each plot (not just aggregated data per successional age). Studies measuring only species occurrence or cover-abundance (Kassi N'Dja and Decocq 2008) were not considered. The inclusion of a study was ultimately dependent on the agreement of authors to provide raw data.

Data preparation and exploration

Some selected studies included sets of plots (referred to as 'datasets') with different previous land uses, soil and/or vegetation types, with each of the datasets independently meeting the inclusion criteria. These datasets were considered as independent units in our meta-analyses.

Some datasets focused only on dicot trees and shrubs while others also considered palms, lianas, cacti and herbs. To remove this possible source of difference between datasets, we excluded life forms other than dicot trees and shrubs from all the floristic tables. Plots with missing information (e.g. successional age, previous land use) or with no trees or shrubs were also removed from the datasets. Some studies used nested subplots of different sizes within each plot for different tree size categories, with a coherent design for all successional ages. In these cases, the number of individuals of each species per subplot was scaled to the size of the plot, using the method of Lebrija-Trejos et al. (2010) and values per size category summed. When the raw data gave the size or size class of individual stems, we excluded stems below the range of minimum diameters that we imposed to maximise consistency across the studies (Table 1).

For each plot in every dataset, we calculated the species richness and Shannon evenness index. To account for the differences in number of stems between plots, within and across datasets, we standardised species richness to a fixed number of stems (15), following the method proposed by Colwell et al. (2012). We selected the number 15 to avoid standardising to more than three times the actual number of stems (the limit recommended by Colwell et al. 2012) for 98.5% of the plots. Standardised Shannon and Simpson diversity indices, which combine richness and evenness (Magurran 2005), were also calculated but their meta-analyses gave qualitatively similar results to those for species richness so we do not present these results. To investigate the compositional similarity between successional plots and old-growth reference plots in the same dataset, we calculated the Sørensen index (based on species occurrence) and the version of the Chao–Sørensen index (based on species abundance) that is not adjusted for missing species. For any pair of successional and old-growth plots, the Sørensen index is $2S_{12}/(S_1 + S_2)$ where S_{12} is the number of shared species, S_1 is the number of species in the successional plot and S_2 in the old-growth plot, and the Chao–Sørensen index is $2UV / (U + V)$ where U is the total relative abundance of the shared species in the successional plot, and V in the old-growth plot (Chao et al. 2005). These two indices differ in giving more (Sørensen) or less (Chao–Sørensen) relative weight to rare species. When several old-growth plots were available within a dataset, the similarity indices were calculated separately for each plot and averaged. Calculations were performed using the packages VEGAN (Oksanen et al. 2015) and INEXT (Hsieh et al. 2015) in R ver. 3.2.3 (<www.r-project.org>). When the successional age was provided as a range, we used the midpoint of the range. For each dataset, relationships between successional age and each index were visually explored by fitting local polynomial regressions (function LOESS in R) (Cleveland et al. 1992) (Supplementary material Appendix 1 Fig. A1) to get a preliminary understanding of the trends observed for each dataset.

To investigate the source of heterogeneity between datasets, we retrieved values for the following variables from the publications or asked the authors when necessary: previous land use, mean annual precipitation (MAP), number of dry months (precipitation $<$ 100 mm) and duration of succession studied (defined as age of the oldest successional plot). Climatic data were checked with online data provided by local meteorological institutes. We also calculated the ratio of annual potential evapotranspiration to MAP (PET/MAP) as a measure of water availability, using PET data computed with the FAO Penman – Monteith method for the period 1961–1990 (downloaded from <www.fao.org/geonetwork/srv/en/> on 24 January 2016). We used information on soil taxonomy provided in each publication to categorise the datasets into two soil fertility groups, low and high. In brief, we assumed that highly weathered soils described as ultisols or oxisols (ferrosols) were depleted in nutrients, and geologically younger soils, including entisols, inceptisols, alfisols and/or mollisols, had higher fertility. The surrounding landscape is also very likely to influence the process of succession but the absence of sufficient information in the reviewed studies did not allow this to be tested.

Table 1. Datasets included in the meta-analyses of successional tropical dry forests. Shifting means shifting cultivation, MAP is the mean annual precipitation, PET is the annual potential evapotranspiration. The threshold for a dry month is <100 mm of monthly precipitation. The crosses in the last four columns indicate which meta-analyses each dataset was included in. For datasets using a nested design, the plot area is the largest one used in the dataset. The number of plots refers to successional plots only (it excludes old-growth forest plots). This information refers to the data used in the meta-analysis, after data preparation, and can therefore differ slightly from those reported in the original publications.

												Meta-analysis			
Dataset	No. of plots	Plot area (m^2)	Nested design	Minimum DBH (cm)	Duration of succession studied	Previous land use	MAP (mm)	No. of dry months	PET (mm)	Soil fertility class	Country	Richness	Shannon evenness	Sørensen similarity	Chao-Sørensen similarity
Castellanos-Castro and Newton 2015 – Ceibal – pasture	21	100	no	2.5	7–27.5	pasture	900	5	1573	high	Colombia	X	X		
Castellanos-Castro and Newton 2015 – Rosales – pasture	8	100	no	2.5	3.5–20	pasture	900	5	1573	high	Colombia	X	X		
Castellanos-Castro and Newton 2015 – Rosales – shifting	10	100	no	2.5	3.5–15	shifting	900	5	1573	high	Colombia	X	X		
Kennard 2002	60	1000	yes	5	5–50	shifting	1129	6	1701	high	Bolivia	X	X		
Lebrija-Trejos et al. 2008	14	400	yes	1	3–60	shifting	900	7.5	1799	high	Mexico	X	X	X	X
Leiva et al. 2009	100	500	no	5	10–60	pasture	1575	5.5	1426	high	Costa Rica	X	X	X	X
Mora et al. 2015	8	500	no	2.5	1–10	pasture	788	7	1510	no data	Mexico	X	X	X	X
Powers et al. 2009 – Palo Verde TDF	19	1000	no	10	7–60	pasture	1492	5	1484	high	Costa Rica	X	X		
Powers et al. 2009 – Santa Rosa oak	16	1000	no	10	5–30	pasture	1575	5.5	1453	low	Costa Rica	X	X		
Powers et al. 2009 – Santa Rosa TDF	22	1000	no	10	6–60	pasture	1575	5.5	1453	high	Costa Rica	X	X	X	X
Rico-Gray and Garcia-Franco 1992	4	1000	no	1	10–40	shifting	950	7	1594	high	Mexico	X	X	X	X
Sovu et al. 2009	290	100	no	1	1–19	shifting	1647	6	1368	high	Laos	X	X		
Spittler 2001	257	154	no	5	6–50	pasture	1575	5.5	1469	high	Costa Rica	X	X	X	X
												13	**13**	**6**	**6**

Our search and selection gave thirteen datasets from nine studies published between 1992 and 2015, all using a chronosequence approach. Table 1 lists the datasets and provides information on the environment and study design, as well as the number of datasets included in each meta-analysis. Six datasets provided data on both successional and old-growth forests, allowing calculation of the indices of similarity between successional stages and old-growth forests. The number of plots per dataset, excluding old-growth references, ranged from 4 to 290 (median 19). Plot area ranged from 100 to 1000 m^2 (median 500). The minimum diameter at breast height (DBH) for inclusion of trees and shrubs ranged from 1 to 10 cm (median 2.5). Six datasets covered a duration of succession ≤ 30 years and seven > 30 years (maximum 60 years). The previous land uses were pasture (eight datasets) and shifting cultivation (five datasets). MAP ranged from 788 to 1647 mm (median 1129 mm), the number of dry months from 5 to 7.5 (median 5.5) and the ratio PET/MAP from 0.831 to 1.999 (median 1.507). The soil fertility was high for 11 of the 12 datasets for which we had data, so we did not use this variable in the meta-analyses. Most of the datasets were collected in North and Central America (five from Costa Rica and three from Mexico). Four datasets were from South America (three from Colombia and one from Bolivia) and one from Asia (Laos).

Meta-analyses

We performed meta-analysis for each index of species richness, evenness and compositional similarity, using the METAFOR package (Viechtbauer 2010) in R ver. 3.2.3. The effect size (response variable of the meta-analysis) was the estimate of the slope of the linear regression of the considered index against successional age, calculated for each dataset (Rosenberg et al. 2013). Meta-analyses are therefore fitted on a maximum of 13 datasets (Table 1). Successional trends showed various shapes (Supplementary material Appendix 1 Fig. A1), yet linear relationships provided a good approximation across datasets. Their slopes are an effect size that can be analysed by a meta-analysis approach to show the directionality and rate of trends across datasets. Assumptions of normality of residuals and homogeneity of variance of the linear regressions were met (checked graphically). The effect sizes and associated variances, and the goodness of fit (R^2), for each index and dataset are presented in Supplementary material Appendix 2 Fig. A2 and Appendix 3 Table A3 respectively.

We first fitted meta-analyses using random-effect models to account for heterogeneity between datasets due to ecological and methodological differences (random models include a dataset-specific variation) (Mengersen et al. 2013). Second, to investigate reasons for heterogeneity between datasets, we fitted meta-regressions, a type of meta-analysis using moderators (i.e. fixed factors: previous land use, MAP, number of dry months, PET/MAP and duration of succession studied in the dataset) to explain the differences among datasets (Mengersen et al. 2013). Meta-regressions were fitted with mixed-effect models to account for heterogeneity between datasets. Ideally, all moderators would be included in a single model but we had to fit separate models for each moderator to avoid over-fitting due to the small number of available datasets. Duration of succession studied was considered as a categorical variable with two values ($\leq$ or >30 years) because we observed an inflection of the nonlinear relationships between indices and successional age around that age for several studies (Supplementary material Appendix 1 Fig. A1). Meta-analysis and meta-regression models were fitted using the restricted maximum likelihood (REML) estimation method. Datasets were weighted by the inverse of the variance of the estimate of the slope of the linear regression to account for statistical precision of the effect size of each datasets (Koricheva and Gurevitch 2013). Heterogeneity between datasets was tested with the Cochran Q test for meta-analyses and Q-E test for meta-regressions (Cochran 1954).

We used two methods to test for publication bias and robustness of the significant results: graphical observation of funnel plots (Light and Pillemer 1984) and fail-safe number (Rosenberg 2005). In brief, a funnel plot is a plot of the effect size of each dataset against a measure of its variance (here standard error). In the absence of publication bias the plot has a funnel shape symmetric around the mean effect, because the variability and range of effect sizes decreases with decreasing standard error (Jennions et al. 2013). The fail-safe number is the number of datasets with null effect that need to be added to lose the significance of the estimated effect size (at $p = 0.05$). Results are considered robust if the fail-safe number is greater than $5N + 10$, N being the number of datasets included in the analysis for the considered moderator (Rosenthal 1979).

Data deposition

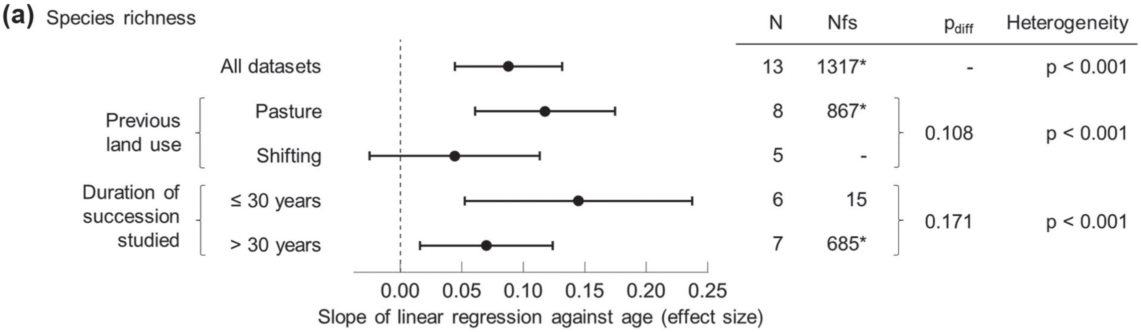
Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.r47tm> (Derroire et al. 2016c).

Results

Species richness and evenness indices

Overall, the species richness and Shannon evenness indices had positive effect sizes, meaning that they increased with succession (Fig. 1, Supplementary material Appendix 4 Table A4), however, the trend observed for Shannon evenness index was not observed when using Simpson evenness index (data not shown). For both indices, the effect sizes were higher for sites previously used as pasture than for shifting cultivation (for the latter they were not significantly different from 0), although the difference between them was significant for Shannon evenness index ($p = 0.003$) but not for species richness ($p = 0.108$). Contrary to expectation, effect sizes were not significantly correlated with the MAP, the number of dry months or PET/MAP (Supplementary material Appendices 4 Table A4 and 5 Fig. A5), indicating that the rate of change in species richness and evenness indices with succession was not significantly dependent on precipitation regime or water availability. For Shannon evenness index, datasets with a duration of succession studied > 30 years showed a significantly higher effect size than shorter-term datasets (for which the effect size was not significantly

(a) Species richness



(b) Shannon evenness index

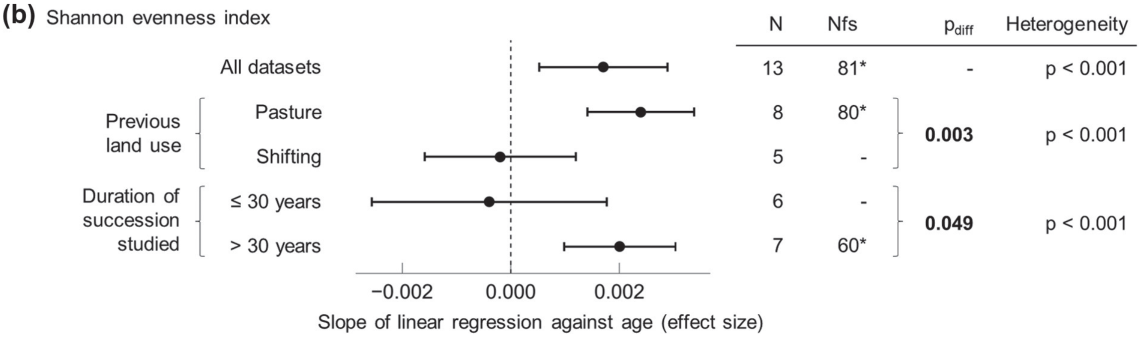


Figure 1. Estimated effect sizes (slope of the linear regression against successional age) of one meta-analysis (all datasets) and two meta-regressions (with previous land use and duration of succession studied) for (a) species richness (standardized to 15 individuals) and (b) Shannon evenness index, from meta-analysis of tropical dry forest datasets. The error bars indicate 95% confidence intervals. The estimate of effect size is significant if the confidence interval excludes 0. N is the number of datasets for each case. Nfs is the fail-safe number for the significant effect size: it assesses the number of datasets with a null estimate that would need to be added to make the result non-significant. The estimate is robust if $Nfs > 5N + 10$ (indicated with an asterix). p_{diff} is the p-value for the significance of the difference between two modalities of a moderator. Heterogeneity between datasets is tested with Cochran's Q test for meta-analysis without moderators and with the Q-E test for meta-regression with moderators, a significant p-value indicates heterogeneity. Shifting means shifting cultivation.

different from zero), suggesting that evenness increases faster in the later stages of succession. However, there was no significant effect of the studied duration of succession for species richness. For the two indices, the Cochran Q and Q-E tests showed a high heterogeneity between all datasets and also between datasets with the same previous land use or duration of succession studied (Fig. 1). Funnels plots did not reveal publication bias for any of the meta-analyses (Supplementary material Appendix 6 Fig. A6) and the fail-safe numbers showed good robustness for all significant effect sizes (Fig. 1), except for the effect size of species richness calculated for data sets with a studied duration of succession ≤ 30 years.

Similarity with old-growth forest

Overall, the effect size of both the Sørensen and Chao–Sørensen indices were positive and quite similar (0.008 and 0.009 respectively) but not significant ($p = 0.075$ and $p = 0.143$ respectively) (Fig. 2, Supplementary material Appendix 4 Table A4). For both indices, the effect sizes differed between the two classes of duration of succession studied. For the five datasets > 30 years the effect sizes were significantly positive (0.003 for both indices) and the fail-safe number showed that these results were very robust, indicating that similarity of composition with old-growth forests increases with succession for the longer-duration datasets. For the dataset ≤ 30 years, the effect sizes were also significantly positive for both indices but not robust, probably because there was only a single dataset. The effect sizes were not significantly dependent on previous land use (Fig. 2), MAP, number of dry months or PET/MAP (Supplementary material Appendix 4 Table A4 and Appendix 5 Fig. A5). For both indices, there was a high heterogeneity between datasets (Fig. 2), overall and between datasets with the same previous land use and same category of duration of succession studied. Funnels plots did not reveal publication bias for the significant results (Supplementary material Appendix 6 Fig. A6).

Discussion

Gradual accumulation of species

The gradual increase in species richness revealed by our meta-analysis is in line with the trends generally observed in tropical dry and wet forests (Chazdon et al. 2007, Lebrija-Trejos et al. 2008, Letcher and Chazdon 2009, Quesada et al. 2009, Dent et al. 2013). This shows a gradual colonisation and establishment of tree species during succession (Anderson 2007, Chazdon et al. 2007). For the datasets including old-growth forests, species richness in the plots of greater successional age is close to that of old-growth forests (Supplementary material Appendix 1 Fig. A1). This is consistent with the findings of Martin et al. (2013) who estimated that tropical forests can recover their species richness in about 50 years. This supports the suggestion that

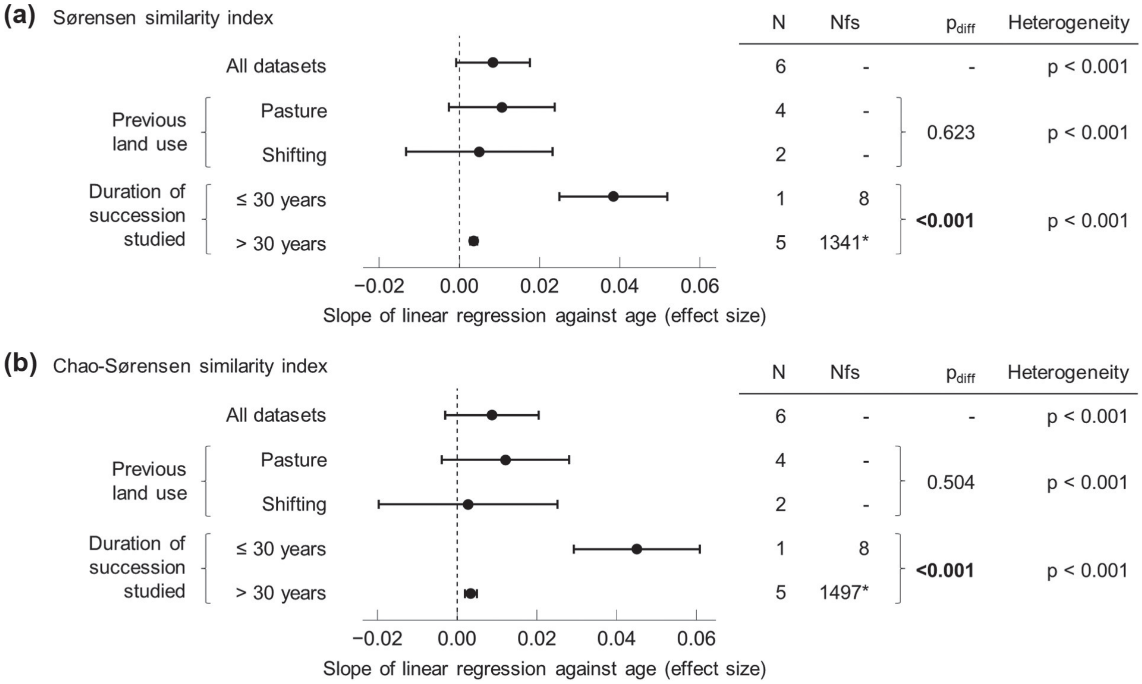


Figure 2. Estimated effect size (slope of the linear regression against successional age) of one meta-analysis (all datasets) and two meta-regressions (with previous land use and duration of succession studied) for (a) the Sørensen and (b) the Chao–Sørensen species composition similarity indices for trees and shrubs, from meta-analysis of tropical dry forest datasets. The error bars indicate 95% confidence intervals. The estimate of the effect size is significant if the confidence interval excludes 0. N is the number of datasets for each case. Nfs is the fail-safe number for the significant effect size: it assesses the number of datasets with a null estimate that would need to be added to make the result non-significant. The estimate is robust if $\text{Nfs} > 5\text{N} + 10$ (indicated with an asterix). p_{diff} is the p-value for the significance of the difference between two modalities of a moderator. Heterogeneity between datasets is tested with Cochran's Q test for meta-analysis without moderators and with the Q-E test for meta-regression with moderators, a significant p-value indicates heterogeneity. Shifting means shifting cultivation.

seed availability is not a major limitation to species colonisation in the considered forests (Vieira and Scariot 2006, Lebrija-Trejos et al. 2008), which can have two non-mutually exclusive explanations: 1) TDF have a high proportion of anemochorous species (Bullock 1995), the dispersal of which is less affected by forest fragmentation (Janzen 2002). 2) The mosaic of secondary forests, old-growth forests and agricultural land with scattered trees described by most studies (Kennard 2002), which is a notable characteristic of Neotropical dry landscapes (Chazdon et al. 2011), seems to ensure a relatively high availability and dispersal of seeds to successional forests (Chazdon 2014). However, it is likely that large-seeded species requiring specialist dispersers may arrive only in the late stages of succession (Lohbeck et al. 2013, Chazdon 2014).

We found no significant effect of the duration of succession studied on the rate of increase in species richness (Fig. 1a). For several datasets, the relationship is quite linear (Kennard 2002, Lebrija-Trejos et al. 2008, Leiva et al. 2009, Powers et al. 2009; Palo Verde and Santa Rosa oak, Mora et al. 2015). A study of the successional dynamics (Lebrija-Trejos et al. 2010) in one of the included datasets (Lebrija-Trejos et al. 2008) showed that the accumulation of old-growth forest species occurs at a faster rate than the loss of early successional species, explaining the increase in species richness even in the later stages. This trend can also be explained by the generalist species, able to establish throughout succession and then persist. Rozendaal and Chazdon (2015) found that such species were abundant in successional tropical wet forests, which is also likely to be the case in TDF where the environmental gradient during succession is less strong (Letcher et al. 2015).

We found an overall increase of Shannon evenness index with succession, and the rate of increase was higher where the previous land use was pasture and for longer duration datasets (Fig. 1). This increase is consistent with observations from tropical wet and dry forests (Saldarriaga et al. 1988, Capers et al. 2005, Ruiz et al. 2005). However, despite the importance of evenness in explanations for the maintenance of species richness in tropical forests (Connell 1978), changes in species evenness with succession are poorly explained. Biotic interactions (competition and facilitation) are likely to drive patterns of evenness because of their effect on species relative abundance, however further evidence is required from studies focused on changes in individual species, and ultimately on the interactions between species.

Convergence toward old-growth forest species composition

The similarity of species composition with old-growth forests increased with succession, as indicated by both the Sørensen and Chao–Sørensen indices when the two classes of duration of succession studied were considered separately (Fig. 2). This is also the trend observed for individual datasets (Supplementary material Appendix 1 Fig. A1, Appendix

2 Fig. A2). There is a convergence toward the composition of old-growth forests, supporting a directional trajectory of succession in TDF. However, the increases of both Sørensen and Chao–Sørensen indices with successional age were slow, and for all datasets the similarity of successional plots with old-growth plots remained low even for the later stages of succession (Supplementary material Appendix 1 Fig. A1). This shows an important uncertainty in the recovery of species composition during succession, as also found by Martin et al. (2013) across tropical forests. The arrival of a given species depends on stochastic events and on the availability of seeds from the surrounding landscape. As a consequence, successional trajectories can be better predicted by considering functional groups rather than species composition, as found in TDF and tropical moist forests (Lebrija-Trejos et al. 2010, Dent et al. 2013). Our results suggest that the recovery of the full species composition of old-growth forests may never occur before the next major disturbance event (Chazdon et al. 2007, Chazdon 2008).

The rate of convergence in species composition is similar when calculated with species occurrence (Sørensen index) and with species abundance (Chao-Sørensen) (Fig. 2), suggesting that there is no notable difference in the rate of establishment of abundant and rare species. This result is surprising: because species that are abundant in old-growth forest are more likely to be abundant in the seed rain, we would have expected the species that are abundant in old-growth forests to establish and reach a high level of abundance during succession faster than rarer species. This finding may be attributable to the high evenness observed for most of the datasets (Supplementary material Appendix 1 Fig. A1).

For both indices, the rate of convergence is much higher for the shorter-duration datasets (≤ 30 years) than for the longer-term datasets, suggesting that the arrival of species present in old-growth forests is important in the early stages of succession. This is in line with the results of Lebrija-Trejos et al. (2010) and Chazdon et al. (2011) (obtained using the same data as Lebrija-Trejos et al. 2008 and Mora et al. 2015, respectively) who observed recruitment of old-growth forest species from the early stages of succession. This is probably due to the rapid recovery of the structure of TDF: Lebrija-Trejos et al. (2008) found that canopy height, plant density and crown cover recovered in less than 15 years in a Mexican TDF and Becknell et al. (2012) showed that above-ground biomass reached its maximum in 30 to 50 years. These rapid structural changes provide suitable micro-environmental conditions (increased shading and decreased temperature) for the establishment of species associated with later stages of succession (Lebrija-Trejos et al. 2010, Chazdon et al. 2011). This is consistent with the study of Letcher et al. (2015) showing a lower rate of habitat specialisation of species in TDF than in wet forests, allowing old-growth forest species to arrive earlier in succession. However, this result could also be an artefact of only one study being analysed for the shorter-duration class, and it needs to be retested once a greater number of studies become available.

Factors affecting the rate of change

We found a high heterogeneity amongst studies in the rates of change in species richness, evenness and composition with successional age (Fig. 1, 2), confirming that time is not the only factor controlling changes during succession. Successional pathways result from a number of interacting factors (Chazdon 2014) that we discuss below.

Our results only showed a significant difference in the direction and rate of change between the two previous land uses, pasture and shifting cultivation, for Shannon evenness (Fig. 1, 2). For species richness, the rate of change was higher in pasture but the difference between the two land uses was not significant ($p = 0.108$). The latter result is consistent with those of Norden et al. (2015) and Poorter et al. (2016), and can be explained by the complexity of the effects of previous and on-going land uses. 1) Cultivation can lead to greater soil erosion (Maass et al. 1988) impeding forest recovery. 2) The presence of remnant trees, reported by all datasets of sites previously under pasture, can affect long-term successional trajectories (Schlawin and Zahawi 2008, Sandor and Chazdon 2014) by their capacity to resprout (Vieira et al. 2006, Sampaio 2007), attract seed dispersers (Guevara et al. 1986) and provide suitable conditions for woody species establishment (Duarte et al. 2010, Derroire et al. 2016a). 3) The intensity and duration of the previous land use are important (Pereira et al. 2003). For sites previously used for shifting cultivation, the number of cultivation cycles can affect successional trends (Sovu et al. 2009). Moreover, several land uses may have occurred before abandonment. For example, the combination of cultivation and grazing is common in shifting cultivation practices in Mexico (Chazdon et al. 2011, Morales-Barquero et al. 2015). 4) Perturbation after abandonment of agriculture can also affect the composition of successional forests. Powers et al. (2009) suggest that the abundance of the cattle-dispersed species *Guazuma ulmifolia* in the Palo Verde site in Costa Rica can be attributed to the presence of cattle at that site and that its abundance results in the lowest levels of species richness of the three sites considered in this study, and the lowest rates of their recovery (Supplementary material Appendix 1 Fig. A1, Appendix 2 Fig. A2). 5) Both types of previous land use can be found in the same landscape (Castellanos-Castro and Newton 2015) enabling seed dispersal between these two types of secondary forest that can result in a homogenization of species composition. 6) The use of fire as a management technique, which was mentioned by some included studies both for shifting cultivation (Rico-Gray and Garcia-Franco 1992, Kennard 2002) and pasture (Leiva et al. 2009, Powers et al. 2009), decreases the ability of trees to resprout and reduces the viability of seeds in the soil seed bank (Kennard et al. 2002, Hooper et al. 2004). Nonetheless, our finding that despite all of these complex interacting factors, there was a faster rate of recovery of species evenness during succession on sites previously under pasture than those used for shifting cultivation does show the potential importance of the legacy effects of past land use. This merits further research focused on factors such as survival of remnant vegetation (Chazdon 2003) and the soil seed bank, and soil condition to improve understanding of the mechanisms and scale of its impact on subsequent secondary succession.

Our results did not show any significant effect of precipitation regime (MAP and number of dry months) or water availability (PET/MAP) on changes in species richness, evenness or composition (Fig. 1, 2). The effect of precipitation and water availability on species presence and abundance is therefore different than their effect on biomass, whose recovery increases with increasing precipitation and water availability (Becknell et al. 2012, Poorter et al. 2016). A possible explanation of our results is that the gradients in precipitation regime and water availability can have several opposing effects. The greater importance of resprouting (McDonald et al. 2010) and facilitation (Callaway and Walker 1997) can lead to a faster accumulation of species in drier sites but this can be mitigated by the smaller pools of species capable of tolerating drought. Moreover, the influence of precipitation regime and water availability on both species accumulation and changes in species composition can be obscured by the importance of the remnant vegetation for resprouting, facilitation and seed availability and dispersion (Chazdon 2014).

Other factors not included in our analysis could explain the heterogeneity of successional trajectories. 1) The position of successional forests in the landscape relative to old-growth forests is important for the input of seeds (Sovu et al. 2009, Chazdon 2014, Arroyo-Rodriguez et al. 2016). The direction of the old-growth forests relative to the dominant winds can also affect the species composition of the dispersed seeds (Janzen 1988, Castillo-Nunez et al. 2011). 2) Soil properties: Powers et al. (2009) found that the species composition and the trajectories of changes in diversity differed between three sites with different soils. 3) Stochastic events probably explain part of the heterogeneity between datasets (Norden et al. 2015).

Methodological considerations

The variation in methodology used by the original studies, in terms of plot size, nested design and minimum stem diameter for inclusion, can partly explain the high heterogeneity between data sets that we observed. However, the potential risk of bias is minimised by the fact that we first calculated an effect size per dataset before combining the datasets in the meta-analyses.

We have chosen to use the slope of linear regressions as a common effect size metric for the meta-analyses as it appeared to be a parsimonious choice (Supplementary material Appendix 1 Fig. A1), although some of these relationships are often non-linear (Quesada et al. 2009, Newton and Cantarello 2015) (Fig. 1, 2, Supplementary material Appendix 1 Fig. A1). Our results therefore show direction and relative rates of change with succession rather than quantitative predictions of indices at a given age. Despite high heterogeneity between studies, these trends were particularly robust, which allows them to be interpreted as global trends in TDF, while giving consideration to the geographical bias mentioned hereafter.

The majority of the studies that we found were conducted in the Neotropics (and especially in Mexico and Costa Rica) (Table 1), which is also the case for other meta-analysis of succession in tropical forests (Becknell et al. 2012, Martin et al. 2013), reflecting the wider trend of unbalanced distribution of ecological studies in the tropics (Stocks et al. 2008, Powers et al. 2011). Because of this geographical bias, caution is required in extrapolating our results to African and Asian dry forests. More studies on successional forests in these regions are greatly needed to assess how their characteristics, such as the smaller overall species pool in Africa (Slik et al. 2015) and differences in disturbance history and forest fauna (Corlett and Primack 2006), affect their rate of recovery.

All the considered studies are based on chronosequences, reflecting the low number of dynamic studies of tropical forest succession (Chazdon et al. 2007). This space-for-time substitution approach has been criticized for the potential biases related to the difficulty of 1) distinguishing patterns associated with succession from those resulting from variation in initial conditions (Pickett 1989), and 2) accounting for the possible correlation between time of abandonment and site conditions (such as soil fertility) (Chazdon 2003). However, they are recognized as a useful approach for assessing long-term direction of change (Lebrija-Trejos et al. 2010). Moreover, Mora et al. (2015) showed by combining chronosequence and dynamic approaches, that chronosequence models had greater power for predicting species-based patterns (diversity and composition) than structural patterns. It is important to recognize, however, that there may be a bias in scientists' choice of study sites towards areas where changes with succession are obvious and therefore easier to quantify, potentially leading to an overestimation of the resilience capacity of TDF. A dynamic approach following succession from its earliest stages would be less subject to this bias.

Conclusions

Meta-analysis of 13 datasets showed directionality and convergence of changes in species richness, evenness and composition of tree and shrub communities with succession. This supports the importance of deterministic processes for successional trajectories in TDF despite large levels of uncertainty (Norden et al. 2015). Our results indicate an overall resilience of TDF species richness, supporting the potential of secondary forests for long-term biodiversity conservation even with on-going periodic severe human disturbance. However, active conservation interventions may still be beneficial because recovery of the species composition of old-growth forests is slow and uncertain, and secondary forests may never reach the same composition as old-growth forests. The high heterogeneity between the datasets reflects the complexity of the interacting factors affecting succession in determining the assembly of secondary forest communities (Chazdon 2003). Succession of TDF is therefore an issue deserving further study. A focus on Asian and African dry forests will be needed to fill the biggest geographical gaps in current evidence. There is also a need for more detailed assessment of the legacy effects of previous land use (Chazdon 2003) and the effect of landscape-scale patterns (Arroyo-Rodriguez et al. 2016).

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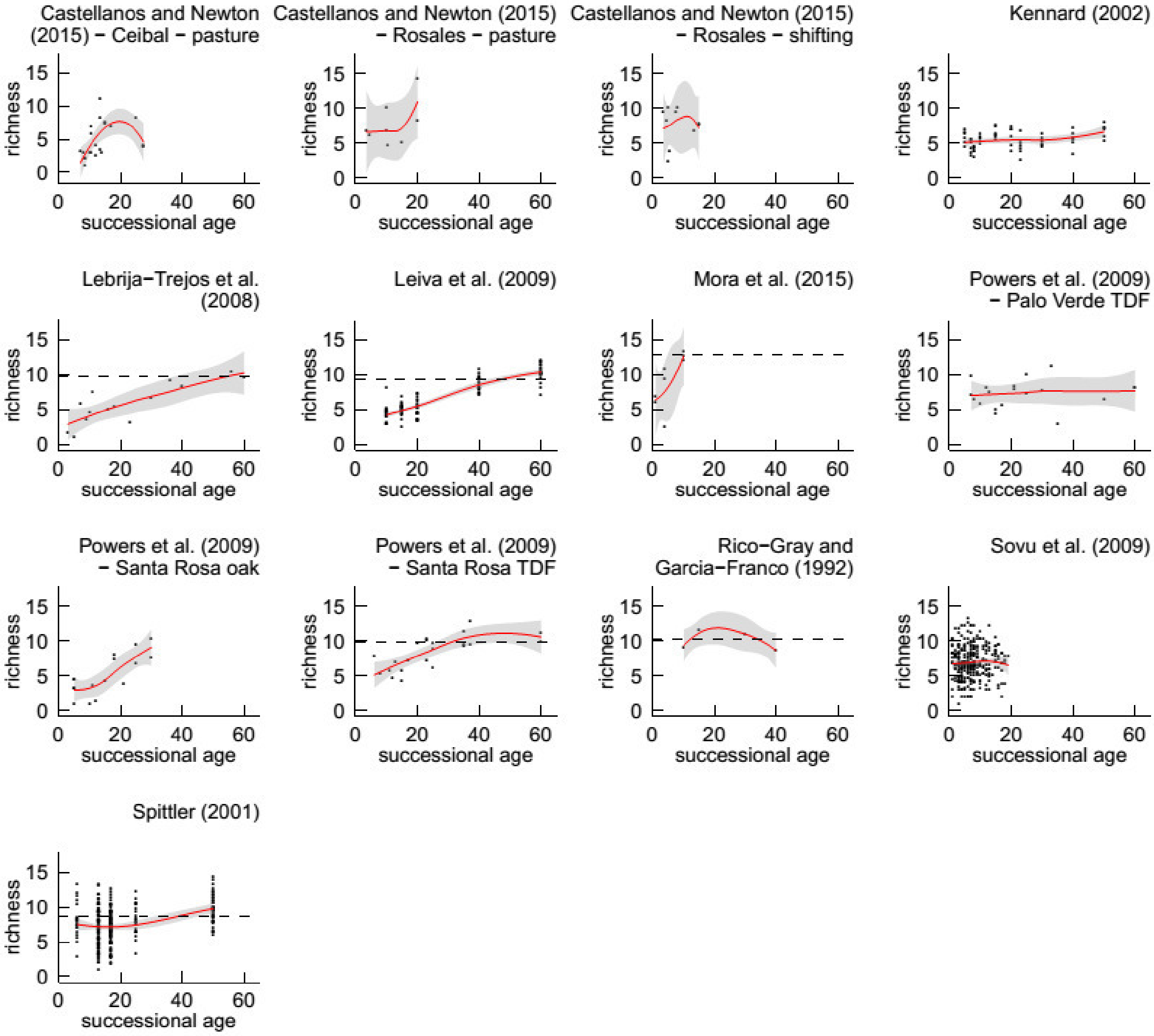
Supplementary material (Appendix oik-03229 at <www.oikosjournal.org/appendix/oik-03229>). Appendix 1–6.

OIKOS

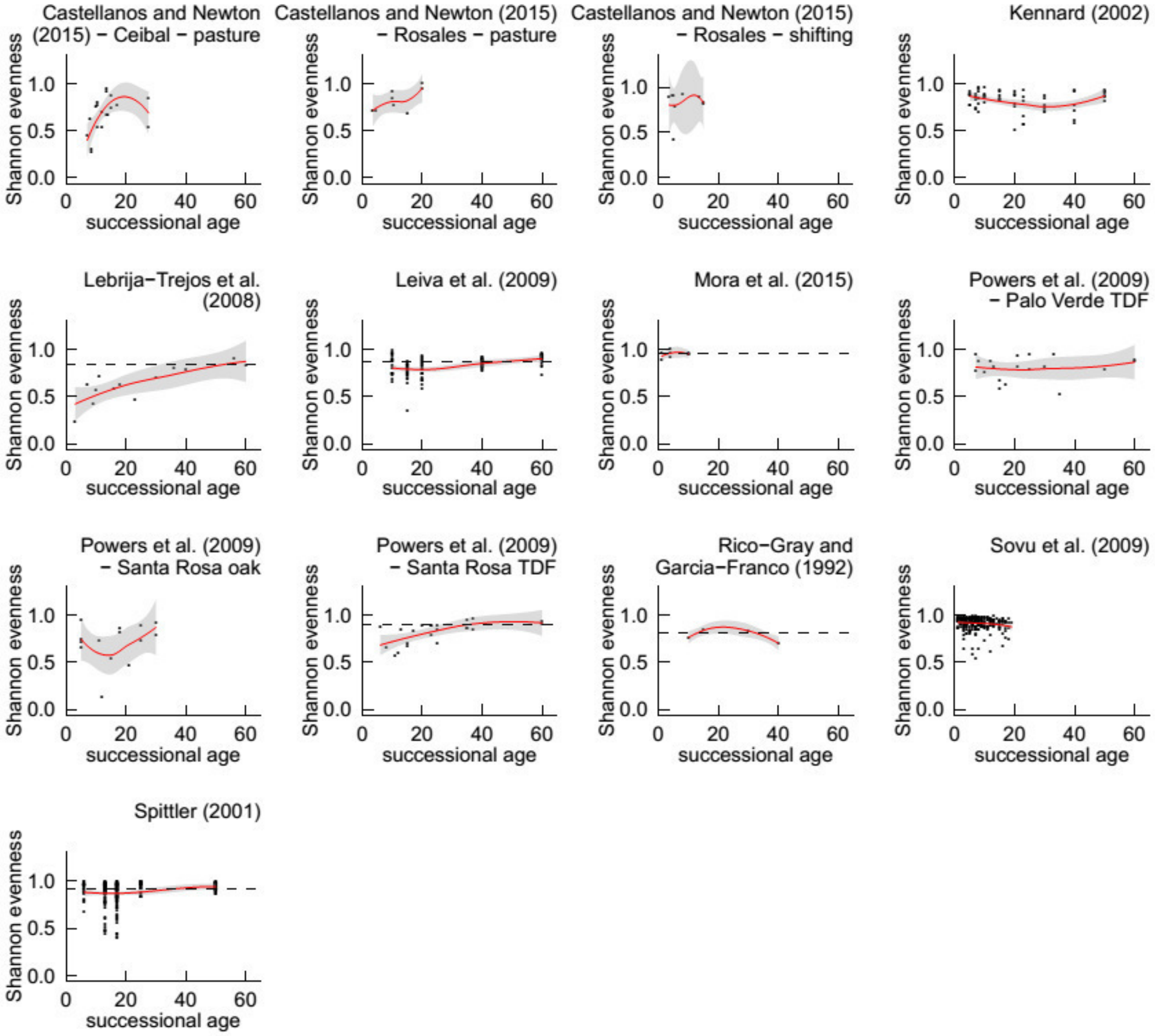
Derroire, G., et al. 2016. Resilience of tropical dry forests – a meta-analysis of changes in species diversity and composition during secondary succession. – Oikos doi: 10.1111/oik.03229.

Appendix 1. Fitted local polynomial regressions of each index of species richness, evenness and composition similarity for tree and shrub species with age of succession in tropical dry forest datasets. The red line is the fitted regression (using function LOESS in R 3.1.3). The grey shading is the area demarcated by the 95% confidence intervals. The dashed line is the mean value for old-growth forest plots, when available. Dots are observations. Castellanos stands for Castellanos-Castro.

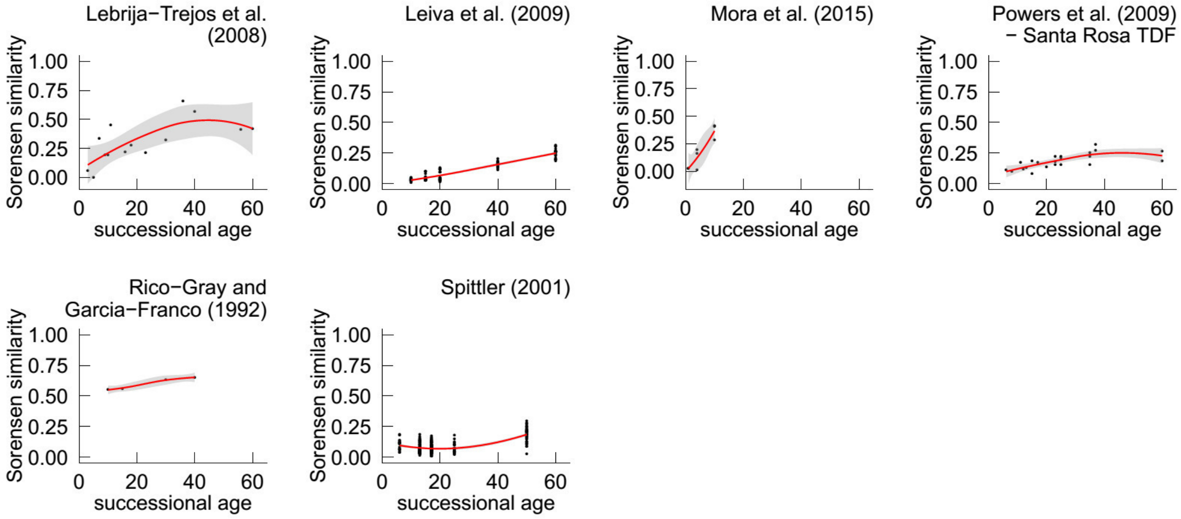
a) Species richness



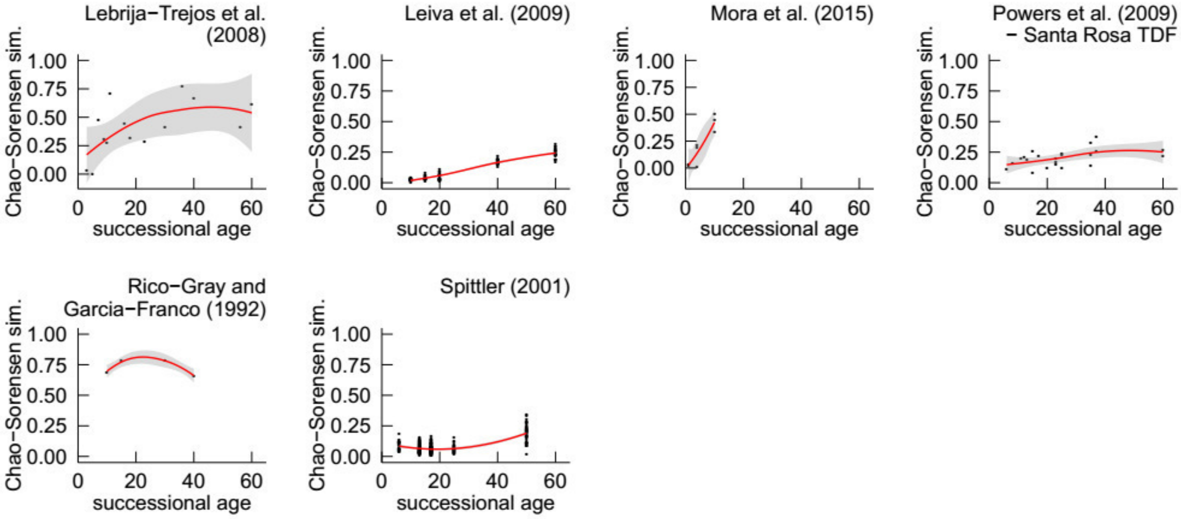
b) Shannon evenness index



c) Sørensen similarity index

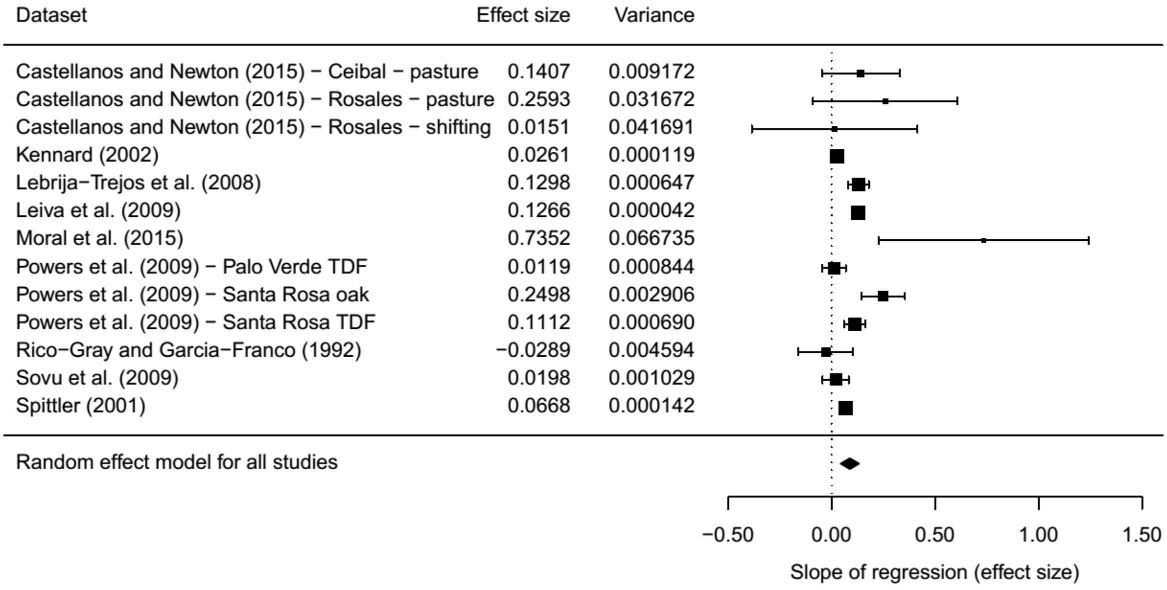


d) Chao-Sørensen similarity index



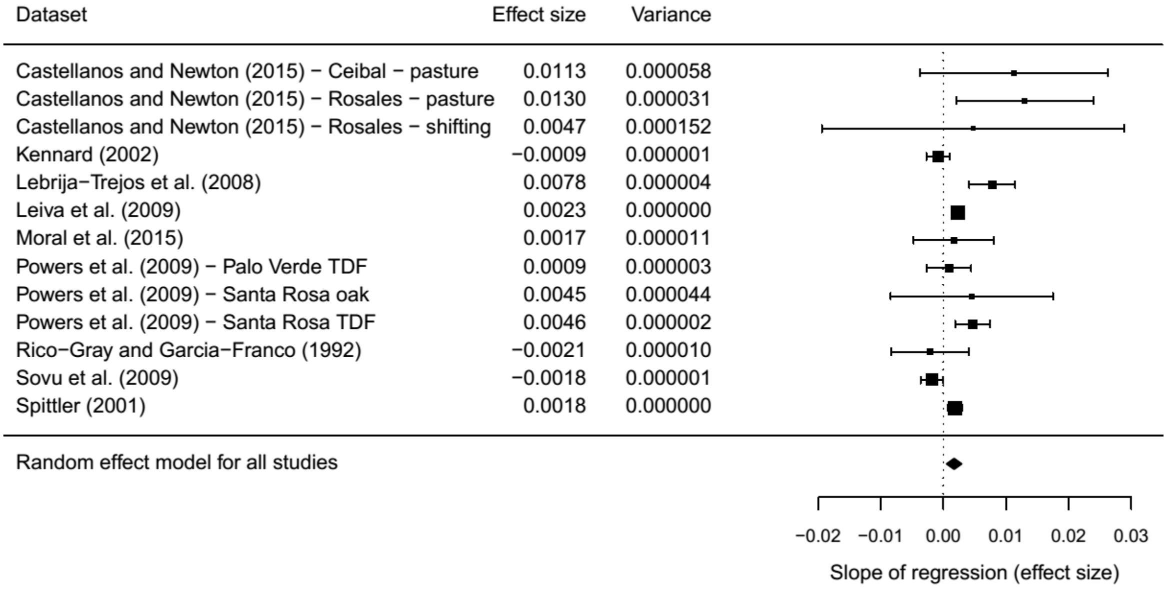
Appendix 2. Forest plot of meta-analysis of the slope of linear regression of the considered index against successional age (effect size) for each index of species richness, evenness and composition of tree and shrub species in successional tropical dry forest. The dashed line represents a slope of zero (no correlation between the considered index and successional age). The size of boxes represents the weight of the study in the analysis. Horizontal lines represent 95% confidence intervals. Positive effect sizes indicate a positive change with successional age. The position of the centre of the diamond represents the overall summary effect (obtained with a random-effect weighted meta-analysis model) and its horizontal extent represents the positive and negative 95% confidence intervals. Castellanos stands for Castellanos-Castro.

a) Species richness



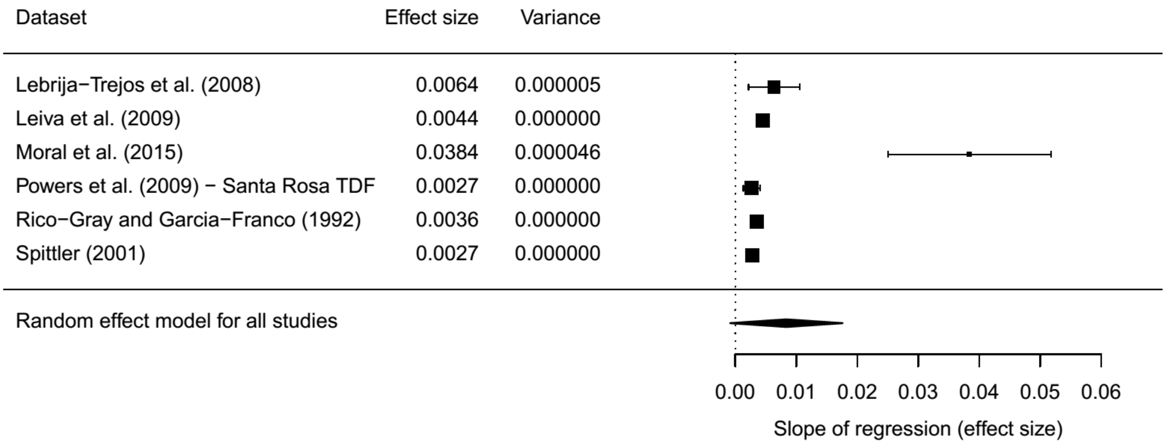
Dataset	Effect size	Variance
Castellanos and Newton (2015) − Ceibal − pasture	0.1407	0.009172
Castellanos and Newton (2015) − Rosales − pasture	0.2593	0.031672
Castellanos and Newton (2015) − Rosales − shifting	0.0151	0.041691
Kennard (2002)	0.0261	0.000119
Lebrija−Trejos et al. (2008)	0.1298	0.000647
Leiva et al. (2009)	0.1266	0.000042
Moral et al. (2015)	0.7352	0.066735
Powers et al. (2009) − Palo Verde TDF	0.0119	0.000844
Powers et al. (2009) − Santa Rosa oak	0.2498	0.002906
Powers et al. (2009) − Santa Rosa TDF	0.1112	0.000690
Rico−Gray and Garcia−Franco (1992)	−0.0289	0.004594
Sovu et al. (2009)	0.0198	0.001029
Spittler (2001)	0.0668	0.000142
Random effect model for all studies		

b) Shannon evenness index



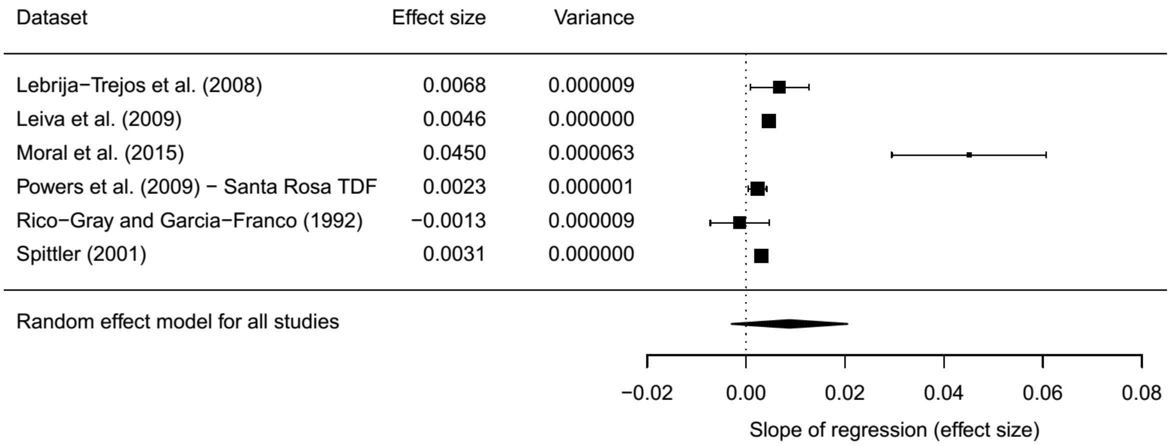
Dataset	Effect size	Variance
Castellanos and Newton (2015) − Ceibal − pasture	0.0113	0.000058
Castellanos and Newton (2015) − Rosales − pasture	0.0130	0.000031
Castellanos and Newton (2015) − Rosales − shifting	0.0047	0.000152
Kennard (2002)	−0.0009	0.000001
Lebrija−Trejos et al. (2008)	0.0078	0.000004
Leiva et al. (2009)	0.0023	0.000000
Moral et al. (2015)	0.0017	0.000011
Powers et al. (2009) − Palo Verde TDF	0.0009	0.000003
Powers et al. (2009) − Santa Rosa oak	0.0045	0.000044
Powers et al. (2009) − Santa Rosa TDF	0.0046	0.000002
Rico−Gray and Garcia−Franco (1992)	−0.0021	0.000010
Sovu et al. (2009)	−0.0018	0.000001
Spittler (2001)	0.0018	0.000000
Random effect model for all studies		

c) Sørensen similarity index



Dataset	Effect size	Variance
Lebrija−Trejos et al. (2008)	0.0064	0.000005
Leiva et al. (2009)	0.0044	0.000000
Moral et al. (2015)	0.0384	0.000046
Powers et al. (2009) − Santa Rosa TDF	0.0027	0.000000
Rico−Gray and Garcia−Franco (1992)	0.0036	0.000000
Spittler (2001)	0.0027	0.000000
Random effect model for all studies		

d) Chao-Sørensen similarity index



Dataset	Effect size	Variance
Lebrija−Trejos et al. (2008)	0.0068	0.000009
Leiva et al. (2009)	0.0046	0.000000
Moral et al. (2015)	0.0450	0.000063
Powers et al. (2009) − Santa Rosa TDF	0.0023	0.000001
Rico−Gray and Garcia−Franco (1992)	−0.0013	0.000009
Spittler (2001)	0.0031	0.000000
Random effect model for all studies		

Appendix 3. Goodness of fit (R^2) of the linear regressions fitted for each index and datasets.

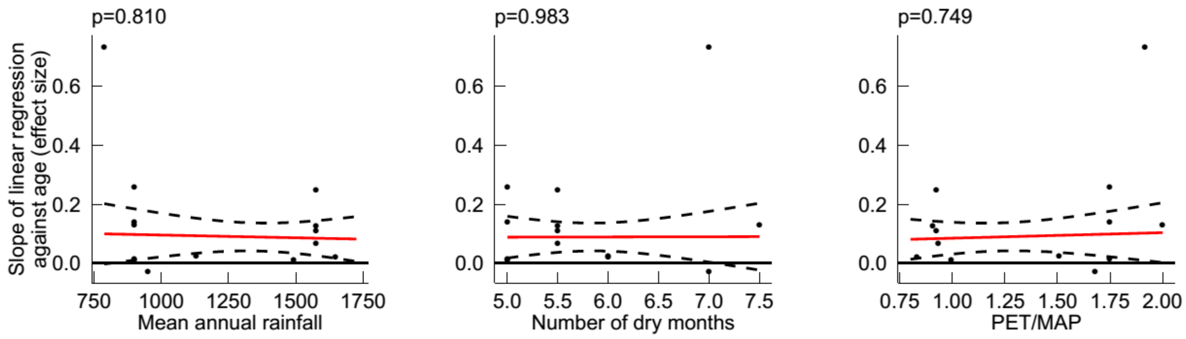
Dataset	Goodness of fit (R2) for Species richness	Shannon evenness	Sørensen similarity	Chao-Sørensen similarity
Castellanos-Castro and Newton (2015) - Ceibal - pasture	0.102	0.113	-	-
Castellanos-Castro and Newton (2015) - Rosales - pasture	0.261	0.474	-	-
Castellanos-Castro and Newton (2015) - Rosales - shifting	0.001	0.020	-	-
Kennard (2002)	0.089	0.014	-	-
Lebrija-Trejos et al. (2008)	0.684	0.608	0.424	0.297
Leiva et al. (2009)	0.795	0.176	0.894	0.910
Mora et al. (2015)	0.574	0.041	0.841	0.842
Powers et al. (2009) - Palo Verde TDF	0.010	0.014	-	-
Powers et al. (2009) - Santa Rosa oak	0.605	0.038	-	-
Powers et al. (2009) - Santa Rosa TDF	0.472	0.349	0.421	0.224
Rico-Gray and Garcia-Franco (1992)	0.083	0.188	0.972	0.080
Sovu et al. (2009)	0.001	0.014	-	-
Spittler (2001)	0.110	0.040	0.378	0.432

Appendix 4. Results of meta-analyses (all datasets) and meta-regressions of the slope of linear regression of the considered index against successional age (effect size) for each index of species richness, evenness and composition of tree and shrub species in successional tropical dry forest. MAP is mean annual precipitation and PET/MAP is the ratio between annual Potential Evapotranspiration and MAP. The estimates of effect size in bold are significant (the 95% confidence interval excludes 0). For the meta-regressions on categorical moderators (previous land use and duration of succession studied), p-values give the significance of the difference between the two categories. For the meta-regressions on continuous moderators (MAP, number of dry months and PET/MAP), p-values give the significance of the relationship between the effect size and the continuous moderators.

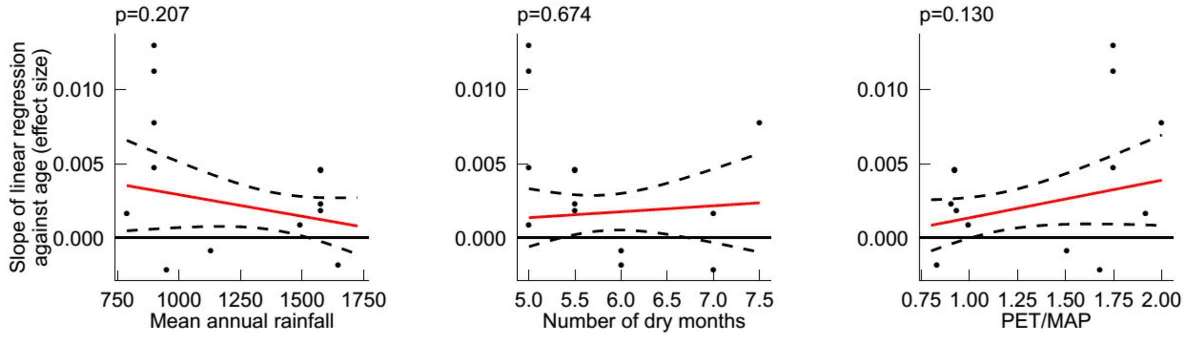
		Species richness	Shannon evenness	Sørensen similarity	Chao-Sørensen similarity
All datasets	effect size	**0.088**	**0.002**	0.008	0.009
Previous land use	effect size pasture	**0.118**	**0.002**	0.011	0.012
	effect size shifting	0.044	-0.0002	0.005	0.003
	p-value	0.108	0.003	0.623	0.504
Duration of succession studied	effect size ≤ 30 years	**0.145**	-0.0004	**0.038**	**0.045**
	effect size > 30 years	**0.070**	**0.002**	**0.003**	**0.003**
	p-value	0.171	0.049	<0.001	<0.001
MAP	slope of meta-regression	-0.0000	-0.0000	-0.0000	-0.0000
	p-value	0.810	0.207	0.143	0.213
Number of dry months	slope of meta-regression	0.001	0.0004	0.005	0.006
	p-value	0.983	0.674	0.363	0.449
PET/MAP	slope of meta-regression	0.019	0.002	0.012	0.014
	p-value	0.749	0.130	0.203	0.268

Appendix 5. Results of the meta-regressions of the slope of linear regression of the considered index against successional age (effect size) for each index of species richness, evenness and composition of tree and shrub species and each continuous moderator, in successional tropical dry forest. PET/MAP is the ratio between annual Potential Evapotranspiration and the Mean Annual Precipitation. The red line is the meta-regression, the dashed lines the 95% confidence interval and dots are the effect size for the datasets. P-values give the significance of the relationship between the effect size and the continuous moderators.

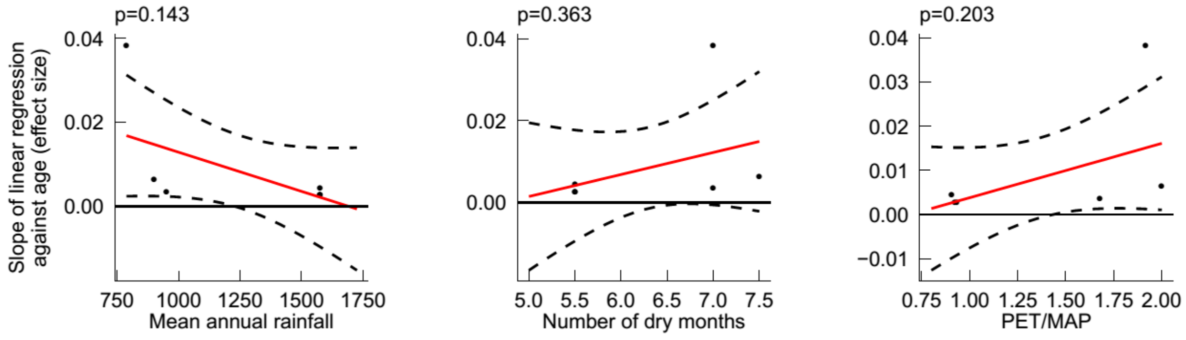
a) Species richness



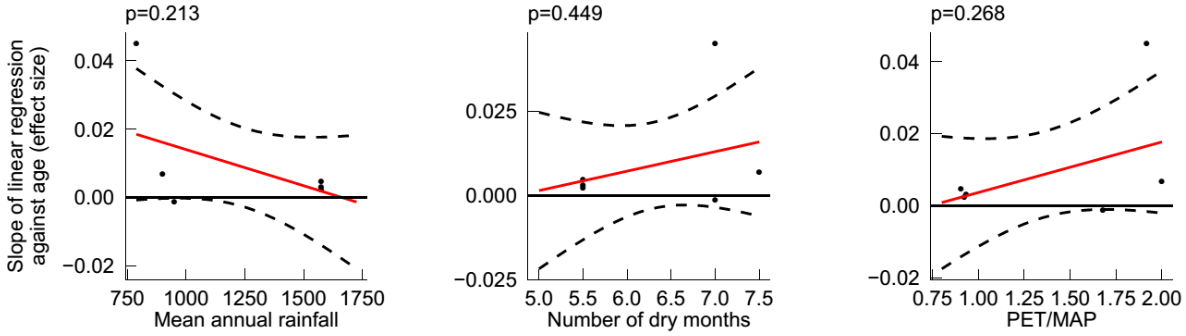
b) Shannon evenness index



c) Sørensen similarity index

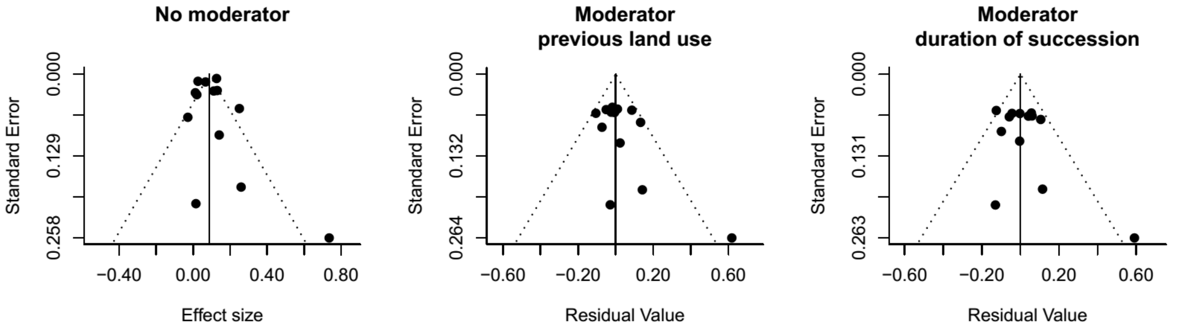


d) Chao-Sørensen similarity index

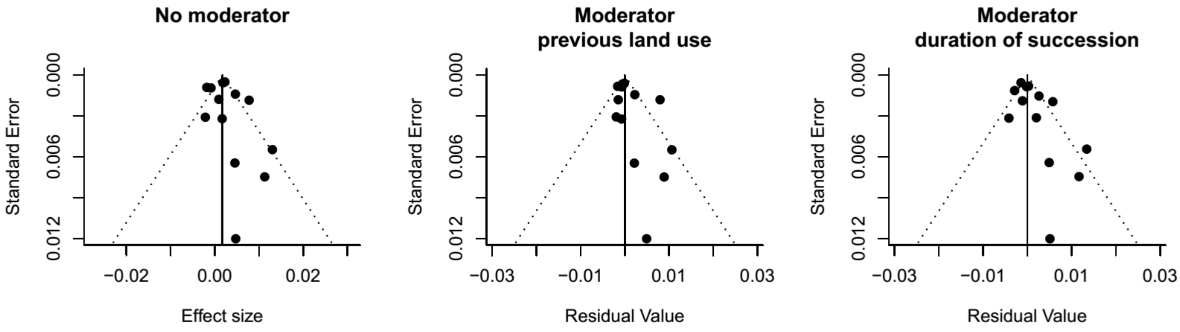


Appendix 6. Funnel plots for the overall analysis (without moderators) of the slope of linear regression of the considered index against successional age and for the meta-regressions with the moderators previous land use and duration of succession studied, for each index of species richness, evenness and composition of tree and shrub species in successional tropical dry forest. Dashed lines represent 95% pseudo-confidence intervals.

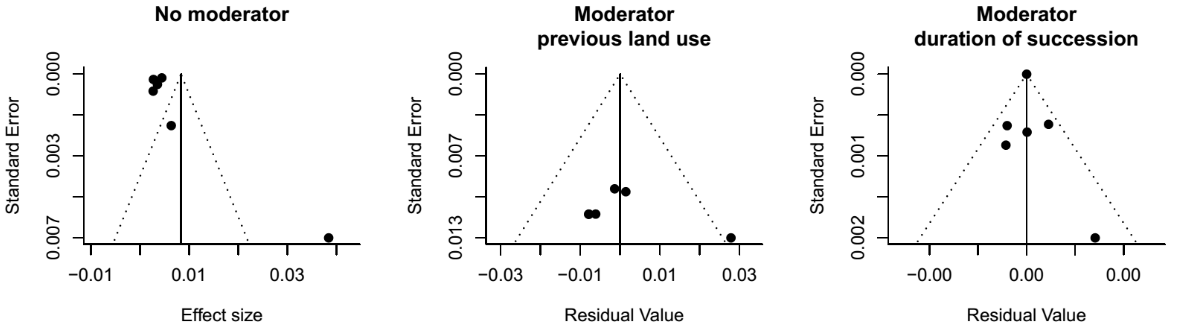
a) Species richness



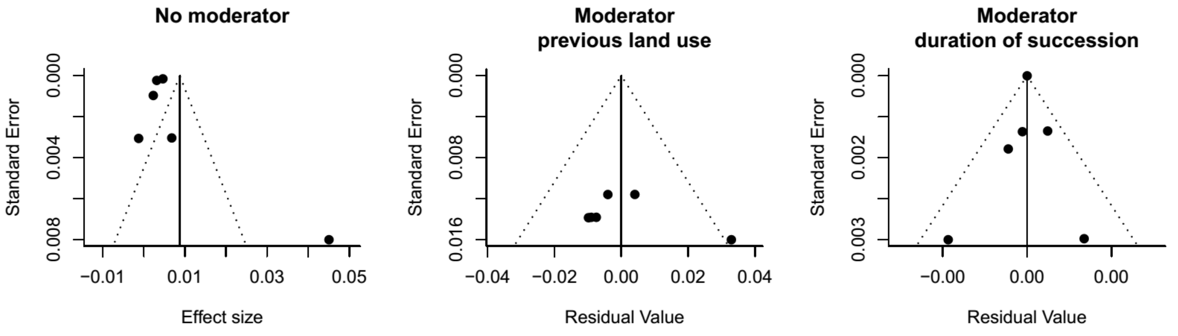
b) Shannon evenness index



c) Sørensen similarity index



d) Chao-Sørensen similarity index



Paper III

Derroire, G., Coe, R., Healey, J.R. (2016). Isolated trees as nuclei of regeneration in tropical pastures: testing the importance of niche-based and landscape factors. *Journal of Vegetation Science*, 27(4), pp. 679-691.

Journal of Vegetation Science **27** (2016) 679–691

Isolated trees as nuclei of regeneration in tropical pastures: testing the importance of niche-based and landscape factors

Géraldine Derroire, Richard Coe & John R. Healey

Keywords
Biodiversity; Community assembly; Costa Rica; Environmental filtering; Facilitation; Plant functional traits; Regeneration; Secondary succession; Seed dispersal; Tropical dry forest

Abbreviation
TDF = Tropical Dry Forests.

Abbreviations for attributes of isolated trees are given in Appendix S1.

Nomenclature
The Plant List (http://www.theplantlist.org/; accessed 15 Jan 2015)

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Abstract

Questions: Our study tests the relative importance of different attributes of isolated trees in explaining the properties of the regeneration assemblage beneath their crowns to evaluate their effect on the composition of early successional stages and understand the processes underlying this effect. We asked: (1) does the regeneration assemblage contain a high proportion of individuals conspecific with the isolated tree; (2) how does the landscape surrounding an isolated tree influence the properties of the regeneration assemblage; and (3) what is the respective importance of structural variables and functional traits of isolated trees for their influence on the properties of the regeneration assemblage?

Location: Three pasture sites in Guanacaste Province, a tropical seasonally dry area, Costa Rica.

Methods: Ninety isolated trees were characterized by their position in the landscape relative to patches of trees, individual structural variables related to tree and crown size, and species functional traits. The assemblage of woody plants regenerating under their crowns was characterized by number of individuals and species, and taxonomic and functional composition. To understand the mechanisms underlying the facilitative effect of isolated trees on regeneration, correlations between their attributes and properties of the regeneration assemblage were assessed.

Results: We found that a low proportion of regenerating individuals were conspecific with the isolated trees beneath which they have established. Landscape factors influenced the regeneration but their effects were site-dependent. The attributes of isolated trees correlated well with the functional composition of the regeneration assemblage: their structure and phenological habits with traits associated with drought tolerance, and their dispersal syndrome with the dispersal syndrome of the regeneration assemblage. However, isolated tree attributes correlated poorly with the regeneration assemblage's taxonomic composition.

Conclusions: Our study shows that an approach based on functional composition can provide a better understanding of community assembly mechanisms than does a taxonomic approach. Two main mechanisms are suggested to explain the influence of isolated trees on the regeneration assemblage: modification of micro-scale environmental conditions (shade and moisture) and influence on dispersal agents. The effect of attributes of isolated trees on the properties of the regeneration assemblage predicts a long-term legacy of the early stages of succession.

Introduction

Conversion of forests into agricultural land is one of the major anthropogenic pressures on tropical forests (FAO 2012). However, socio-economic changes and restoration efforts can reverse this trend and allow secondary forest establishment (Calvo-Alvarado et al. 2009). When cattle farming is abandoned, isolated trees in pastures can promote the natural regeneration of woody forest species and therefore the early stages of succession (Holl et al.

Doi: 10.1111/jvs.12404

2000). The positive role of isolated trees as nuclei of regeneration in abandoned pastures has long been evidenced in tropical wet forest zones (Guevara et al. 1986, 1992; Slocum & Horvitz 2000; Carrière et al. 2002; Schlawin & Zahawi 2008) and to a lesser extent in tropical dry forest zones (Janzen 1988, 2002; Castillo-Nunez et al. 2011; Griscom & Ashton 2011). The mechanisms that underlie the facilitative effects of isolated trees are thought to be mainly facilitation of seed dispersal by attraction of dispersal agents (Guevara et al. 1986) and facilitation of germination and seedling establishment by amelioration of microclimate (Duarte et al. 2010).

Several studies suggest that isolated trees may differ in their positive effect on regeneration: their attributes can influence the number of individuals and species (Guevara et al. 1986; Slocum & Horvitz 2000; Slocum 2001) and the taxonomic composition (Duarte et al. 2010) of the assemblage of woody plants establishing under their crown (*i.e.* the regeneration assemblage). Unfortunately, most of these studies were conducted on a very limited number of individuals and species of isolated trees. This leads to a high risk of bias, which makes the understanding of general trends difficult. Moreover, most of these studies characterize the regeneration assemblage only in terms of taxonomic composition and diversity (Slocum & Horvitz 2000; Slocum 2001; Duarte et al. 2010), whereas its functional composition has only been characterized by the seed dispersal syndrome (Guevara et al. 1992). Considering other functional traits of regenerating plants, such as those associated with environmental requirements, could provide a better understanding of the effects of isolated trees on the composition of the regeneration assemblage. Young plants have particularly specific environmental requirements: trees have been found to be more strongly adapted (through functional trait values) to their regeneration niche (*sensu* Poorter (2007)) than their adult niche (Poorter 2007).

Besides these niche-based processes, factors linked to a tree's location relative to surrounding tree patches (referred to here as landscape factors) are also expected to influence regeneration since they are generally linked to seed availability and dispersal (Chazdon 2014). It is important in advancing ecological theory to investigate whether or not these landscape factors act in a similar way across regenerating species, independently of a species' ecological requirements. If they do, they can then be considered as neutral (*sensu* Hubbell 2001), but should not be considered stochastic if they are explainable and predictable (Lebrija-Trejos et al. 2010a). However, if the influence of landscape factors varies with the identity of species or their functional type, then it is non-neutral.

The processes underlying the effect of isolated trees on regeneration remain poorly understood and more studies on the hierarchy of importance of different attributes of isolated trees and of landscape factors that promote this effect (such as Duarte et al. 2010) are needed (Peterson et al. 2014). This is especially true in tropical dry forests, where seasonal water limitation represents a major constraint to regeneration (Maass & Burgos 2011) and the balance of tree seed dispersal syndromes (Vieira & Scariot 2006) has led to the prediction that the effect of isolated trees on regeneration should be different from that in moist forests. Since regeneration under trees in pastures constitutes a very early step in forest recovery, evaluating the importance of attributes of isolated trees for the structuring of the regeneration assemblage will enable assessment of the importance of the legacy of the initial tree composition (Egler 1954), and of the deterministic and predictable character of succession.

Improved understanding of the factors explaining the positive influence of isolated trees on regeneration also has obvious applications in ecological restoration of tropical dry forests, a globally threatened biome (Miles et al. 2006). Important restoration opportunities are provided by the recent trend of abandonment of livestock production in this climatic zone (Calvo-Alvarado et al. 2009) and growing interest in the role of secondary forests in biodiversity conservation (Chazdon et al. 2009). Knowledge about these early-stage regeneration mechanisms can inform practitioners about which traits to use in the selection of species for the role of nurse trees for restoration, especially when using techniques based on the nucleation model of succession (Yarranton & Morrison 1974), which is receiving increasing attention (Rey Benayas et al. 2008; Corbin & Holl 2012).

Our study investigates the factors structuring woody plant regeneration under isolated pasture trees in dry tropical areas. We aim to test the importance of landscape factors and of the attributes of isolated trees acting at a more local scale (individual structural variables and species functional traits) in explaining the properties of the woody plant regeneration assemblage beneath their crowns, by surveying the assemblage under a large sample of isolated trees in active pasture sites in Costa Rica. We ask the following questions: (1) does the regeneration assemblage contain a high proportion of individuals of the same species as the isolated tree beneath whose crown it occurs? Because most tree seeds are dispersed over short distances (up to 200–300 m) from the parent tree in this biome (Janzen 1988), we expect this proportion to be high. However, if the mortality rate of seedlings of the same species as the adult tree is higher than for other species, as predicted by the Janzen-Connell hypothesis (Janzen 1970; Connell 1971), we expect this proportion to be low. (2) Do landscape factors influence the number of individuals and species, the taxonomic composition and the functional

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composition of the regeneration assemblage? If so, what is the most influential landscape factor? We expect landscape factors to be important but do not know over what scale they would have a detectable effect. (3) What is the relative influence of structural variables (e.g. height, crown area) and functional traits of isolated trees on the number of individuals and species, taxonomic composition and functional composition of the early woody regeneration assemblage that occurs beneath their crowns? We predict that the attributes of isolated trees would have two effects: (1) the structural variables and the leaf phenological habit of the isolated trees are expected to influence traits of the regenerating plants linked to resource acquisition (water and light) through their impact on the microenvironment, and (2) the seed dispersal syndrome and structure of the isolated trees are expected to act on dispersal of seeds beneath their crowns by attracting dispersal agents.

Methods

Study site and studied trees

The study was conducted in Guanacaste Province, northwest Costa Rica. The climate is characterized by strong rainfall seasonality with a 5–6 mo dry season and >95% of the ~1700 mm mean annual rainfall falling during the May–Nov wet season (Instituto Meteorológico Nacional de Costa Rica, meteorological station of Liberia 10.58° N; 85.53° W, 1977–2012). The original vegetation is tropical dry forest (TDF; Holdridge et al. 1971). Extensive conversion of these forests to pasture land occurred until the 1980s. Since then, forest conservation policies combined with socio-economic changes have resulted in forest recovery (Calvo-Alvarado et al. 2009) across a mosaic of pastures and secondary forests of different ages.

Three active pasture sites located on private lands were studied: Ahogados (10.80° N, 85.54° W), Lamentos (10.74° N, 85.63° W) and Aromal (10.73° N, 85.60° W; Fig. 1). The age of the pastures (i.e. time since conversion) was at least 45 yr. Qualitative data on the past and present land uses of these sites have been obtained from landowners and managers and are reported in Appendix S1. The pastures are flat and crossed by a number of non-permanent streams lined with riparian vegetation.

We selected a high number of individuals and species of isolated trees to minimize the risk of bias due to phylogenetic correlation amongst traits. We used several inclusion criteria for trees: (1) crown not overlapping with the crown of another tree; (2) no substantial part of the crown

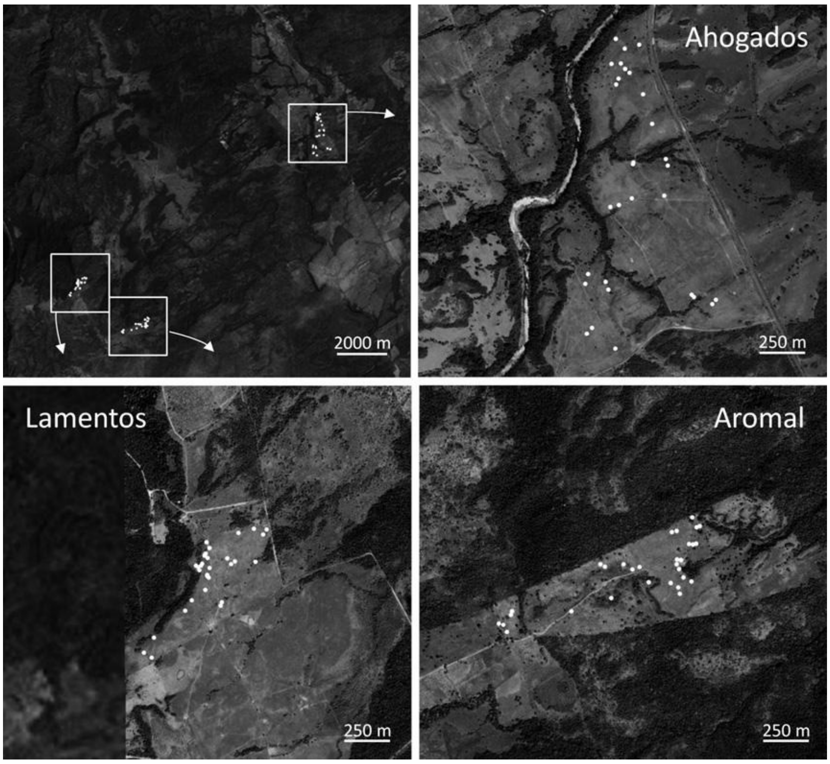

Fig. 1. Positions of the studied pasture sites and trees in the landscape. The upper left panel shows the positions of the three pasture sites (white squares) and the three others show the positions of the studied isolated trees (white dots) within these sites. Orthophoto: ESRI World Imagery - captured in Jan 2011 (Geoeye 2011).

covered by a liana (so that the effects of trees could be separated from lianas); (3) located in an area with environmental conditions comparable to the rest of the site (areas that had hydromorphic soil or recent burning were excluded). We conducted a pre-survey of all isolated trees in each site and estimated their distance to the nearest tree patch (as defined in the section on attributes of isolated trees below), height and crown radius. We then selected 30 trees per site (90 trees from 30 species in total) to match the species mix of all trees present in each site and to cover the full range of values for these three estimated variables.

Attributes of isolated trees

Three types of attributes were quantified for each tree: landscape factors, structural variables of the individual tree and functional traits of its species. We calculated the following landscape factors for each tree: distance to the nearest tree patch (*Distance*), and the area of tree patches in buffers of 100 m ($Area_{100}$), 500 m ($Area_{500}$) and 1000 m ($Area_{1000}$) around the focal isolated tree. To do so, we recorded the coordinates of each tree and used two orthophotos to delimit the trees patches, defined as an area ≥400 m^2 with a predominantly closed canopy of mature trees (riparian vegetation was included), in ArcGIS (ESRI, 1999–2009; see Appendix S1 for details).

We considered the following structural variables for their likely impact of the amount of shade cast by isolated trees, as rigorous measurement of shade was impractical due to its high seasonal dependency: total height (*Height*), height of the bottom of the lowest branch (*Hbranch*), *Crown length*, *Crown area*, *Crown volume*, ratio of crown length:tree height (*RhH*), ratio of crown area:tree height (*RAH*), ratio of crown volume:tree height (*RVolH*), ratio of crown area: crown length (*RAh*) and *Sampling area* delimited by the vertical projection of the tree's crown edge plus a 1-m buffer beyond (details of the measurement and calculation of these variables are provided in Appendix S1).

For the functional traits of isolated trees, three variables were considered. Values of the seed dispersal syndrome (*Dispersal*, two categories: zoochorous vs anemochorous and autochorous) and the leaf phenological habit (*Phenology*, two categories: evergreen and semi-deciduous vs fully deciduous) of the tree species were obtained from data provided in Powers & Tiffin (2010) supplemented with information obtained from local experts (R. Espinoza and D. Perez Avilez, pers. comm.). Information on the capacity to fix nitrogen (*N-fixation*) of all Leguminosae species was obtained from Halliday (1984), Sprent & Parsons (2000), Sprent (2005), Wishnie et al. (2007) and Griscom & Ashton (2011).

Although not strictly an attribute of isolated trees, we used *Site* as a variable qualifying isolated trees because *Site* encompasses a range of non-stochastic factors that have not been measured, such as the intensity of grazing, pasture management practices and variation in soil and hydrology.

Survey and properties of the regeneration assemblage

In July 2013, we conducted a survey of the regenerating woody vegetation under each selected isolated tree. We quantified and identified all seedlings, saplings and young adults of trees, tall shrubs (only shrub species that can grow >2 m in height were considered) and woody lianas located in the *Sampling area*. Individuals sprouting from the roots of the trees (as visually assessed by inspecting the first few centimetres of the tap root) were excluded. The minimum height for a plant to be included was 10 cm, to exclude seedlings germinated in the year of data collection, which have not yet experienced the full annual climatic cycle. We set no upper height limit for inclusion. However, we did not select isolated trees where the relative size of trees with overlapping crowns created any uncertainty about whether the isolated tree established before the woody regeneration located under its crown.

Each species of regenerating woody plant was assigned to one life-form category (trees and shrubs vs woody lianas), leaf structural complexity category (simple vs compound) and taxonomic category (member of Leguminosae family vs not) based on literature (Enquist & Sullivan 2001; Powers & Tiffin 2010) and on-line resources (INBio; http://atta2.inbio.ac.cr and Flora de Nicaragua; http://www.tropicos.org/Project/FN, accessed 10 Dec 2013). Information of leaf phenological habit (evergreen and semi-deciduous vs fully deciduous) and dispersal syndrome (zoochorous vs anemochorous and autochorous) was obtained from the same sources as for the species of isolated tree (see Appendix S1 for details on the choice of categories). For trees and shrubs, leaf phenological habit and leaf complexity were selected as traits that indicate a species' drought tolerance and light-capture strategies (Poorter & Markesteijn 2008), although there are some notable exceptions for leaf complexity (e.g. *Guazuma ulmifolia*). These two traits and membership of the Leguminosae family were not considered for lianas because there is no evidence that they relate to plant strategies in the same way as for trees and shrubs. For some species, we were unable to find information on one or more of these traits, but these species never represented more than 0.8% of the individuals found under a tree or 0.05% of the total number of regenerating individuals.

We characterized the assemblage of regenerating individuals occurring under the crown of each sampled isolated tree using the following properties: proportion of conspecifics (individuals of the same species as the tree), number of individuals, number of species, taxonomic composition (at the species level, i.e. number of individuals per species), and functional composition characterized by life form, seed dispersal syndrome, and for individuals of tree and shrub species only, leaf phenological habit, leaf complexity and proportion of individuals from the Leguminosae family. We excluded regenerating individuals of the same species as the isolated tree above from the calculation of all regeneration properties, except the proportion of conspecifics itself. They are likely to originate from seed produced by that tree, which could influence the results related to mechanism of seed dispersal.

Statistical analysis

The influence of the seed dispersal syndrome of isolated trees on the proportion of conspecifics beneath their crowns was tested using a quasi-binomial GLM with a logit link.

To test the influence of each landscape factor on the number of regenerating individuals, their number of species and their functional composition, we performed simple negative binomial and quasi-binomial GLMs to account for over-dispersion. Models were fitted site-by-site and for one landscape factor at a time, to avoid bias due to collinearity between *Site* and landscape factors (Zuur et al. 2010).

To test the relative influence of the attributes of isolated trees on the taxonomic composition of the regeneration assemblage, we used RDA with a Chord transformation. This method computes axes that best explain the variation of the floristic table and expresses each axis as a linear combination of the 17 attributes of isolated trees (Legendre & Gallagher 2001). The continuous attributes were standardized; the absolute values of the canonical coefficients can therefore be used as a measure of the importance of each explanatory variable for each axis (Borcard et al. 2011). The best model was selected using a forward selection and the adjusted R^2 was retrieved following the method of Borcard et al. (2011).

To test the respective influence of the attributes of isolated trees on the number of individuals, the number of species and the functional composition of the regeneration assemblage, we used multiple GLMs. For structural variables of isolated trees, we considered only *Hbranch*, *RAh* and *RhH*, to avoid bias due to collinearity. For the same reason, we included either (1) *Dispersal* or (2) *Phenology* and *N-fixation* in each analysis, depending on the ecological hypothesis that it was testing. The interactions between *Phenology* and structural variables (*RAh* and *RhH*) were the only ones considered in testing if a potential effect of tree structure could differ between evergreen and deciduous trees, since in TDF leaf phenological habit influences the effect of trees on regeneration (Derroire et al. 2016). We used negative-binomial distributions for count data (number of individuals and number of species) and quasi-binomial GLMs for proportional data (functional composition), to account for over-dispersion. The best models were selected by performing a backward selection based on the Akaike information criterion (AIC) for negative-binomial GLMs and on the quasi-AIC (Burnham & Anderson 2002) for quasi-binomial GLMs.

Details of the statistical analyses and a list of the variables considered for each analysis are presented in Appendix S1. All analyses were performed using the environment and language R (R Foundation for Statistical Computing, Vienna, AT) and the packages MASS (Venables & Ripley 2002) and vegan.

Results

We surveyed regeneration of woody plant species in a total *Sampling area* beneath the crowns of isolated trees of 17 089 m² and recorded 6802 individuals (90.7% tree and shrub species; 9.3% lianas), including individuals conspecific with the isolated tree above. The number of regenerating individuals beneath each isolated tree ranged from 0 to 392 (415 for an outlier tree described in Appendix S3). Details of the regenerating woody plants and isolated trees are provided in Appendices S2 and S3.

The proportion of conspecifics between the isolated trees and the regeneration assemblage beneath their crowns was generally low (mean 5.6% of regenerating individuals) but varied greatly amongst the trees (from 0 to 58.8%). Of the 90 surveyed trees, 58 (64.4%) had no conspecific regenerating individuals and only eight (8.8%), comprising five tree species, had more than 25%. The proportion of conspecifics was not dependent on the seed dispersal syndrome of the tree (GLM $P = 0.876$).

All the properties of the regeneration assemblage (except life form) were correlated with some of the included landscape factors, but these correlations varied with *Site* (Table 1). The number of individuals in the regeneration assemblage decreased with increasing *Distance*, and the number of both individuals and species increased with increasing $Area_{100}$ but not with $Area_{500}$ and $Area_{1000}$. The proportion of individuals of zoochorous species decreased where $Area_{100}$ or $Area_{500}$ increased. The proportion of individuals of compound-leaved species was also generally linked to landscape, increasing with *Distance* and slightly decreasing with $Area_{500}$ and $Area_{1000}$. The proportion of individuals of Leguminosae species also increased with *Distance* and decreased with $Area_{100}$ and $Area_{1000}$.

Table 1. Relationship between landscape factors and properties of the regeneration assemblage in each site.

Landscape Factors	*Site*	Properties of Regeneration Assemblage						
		Number of Individuals	Number of Species	Prop. Trees and Shrubs	Prop. Zoochorous	Prop. Deciduous	Prop. Compound-Leaved	Prop. Leguminosae
Distance	Ahogados	−5.169* (10.68)	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	Aromal	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	Lamentos	n.s.	n.s.	n.s.	n.s.	n.s.	8.760* (25.70)	12.37** (41.54)
$Area_{100}$	Ahogados	1.341*** (26.88)	0.635** (21.62)	n.s.	n.s.	n.s.	n.s.	n.s.
	Aromal	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	Lamentos	n.s.	n.s.	n.s.	−1.587* (26.15)	n.s.	n.s.	−2.047*** (52.14)
$Area_{500}$	Ahogados	n.s.	n.s.	n.s.	n.s.	n.s.	−0.055* (16.46)	n.s.
	Aromal	n.s.	n.s.	n.s.	−0.070* (14.56)	n.s.	n.s.	n.s.
	Lamentos	n.s.	n.s.	n.s.	n.s.	n.s.	−0.075* (27.14)	n.s.
$Area_{1000}$	Ahogados	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	−0.009* (14.56)
	Aromal	n.s.	n.s.	n.s.	n.s.	0.005* (17.40)	n.s.	n.s.
	Lamentos	n.s.	n.s.	n.s.	n.s.	n.s.	−0.049** (34.31)	n.s.

The slope (coefficient) of the GLMs is presented for the model including each landscape factor (explanatory variable) and each of the properties of the regeneration assemblage in turn. Models with $P < 0.001$ are shown as ***, $P < 0.01$ as **, $P < 0.05$ as * and $P > 0.05$ as n.s. (not significant). Slope values are only shown for models with $P < 0.05$. The percentage of deviance explained by each model is given in parenthesis as the goodness of fit. *Prop.* is the 'proportion of' (*i.e.* ratio of the number of individuals with the stated trait value:total number of individuals). The proportions of deciduous, compound-leaved and Leguminosae individuals were calculated for the tree and shrub species only; all other results include all regenerating individuals of tree, shrub and liana species.

The 16 attributes of isolated trees were only weakly linked to the taxonomic composition of the regeneration assemblage under their crowns. The overall R^2 of the best model obtained by RDA was 12.84% ($P < 0.001$). This model kept the explanatory variables *Site*, *$Area_{100}$*, *RhH* and *N-fixation* (Table 2). The canonical coefficients show that *Site* is the most important variable in explaining the three axes retained in the best model.

The selected models explained a high percentage of the deviance of the number of individuals (61.10%) and the number of species (58.16%) in the regeneration assemblage (Fig. 2, Table 3, Appendix S4). Both the number of individuals and the number of species increased with *Log Sampling area* and depended on *Site*. There were more regenerating species under evergreen and semi-deciduous than deciduous trees.

Three aspects of the functional composition of the regeneration assemblage were exclusively linked with the structural variables and functional traits of the isolated trees (Fig. 2, Table 3, Appendix S5): a higher proportion of individuals comprising zoochorous species were found under zoochorous trees (overall R^2 = 11.16%). The proportion of individuals comprising deciduous species was positively correlated with *RhH*, negatively with *Crown area* and was higher under deciduous trees (overall R^2 = 26.52%). The proportion of individuals comprising compound-leaved species increased with *RhH* (overall R^2 = 12.30%). The proportion of individuals comprising Leguminosae species increased with *RhH*, was lower under N-fixing than under non-N-fixing trees and varied with *Site* (overall R^2 = 28.96%). The proportion of individuals comprising tree and shrub species was also strongly linked to *Site* (overall R^2 = 21.97%).

Discussion

Low proportion of conspecificity

We found a low proportion of conspecificity between the isolated trees and the regeneration assemblage beneath their crowns. Moreover, this proportion did not differ significantly between species with different seed dispersal syndromes, suggesting that this low proportion is not likely to result from an event at the dispersal stage. It could be explained by distance and/or density-dependent mortality of regenerating plants close to an adult of the same species, due to high risk of predation and pathogen attack. This hypothesis, first formulated by Janzen (1970) and Connell (1971), has been supported by a high number of experimental studies (Comita et al. 2014). The low proportion of conspecifics predicts a high rate of species replacement, which, together with the high number of species in the regeneration assemblages, supports the importance of isolated trees in early stages of succession (Holl et al. 2000).

Table 2. Results of the RDA performed on the taxonomic composition of the woody regeneration assemblage beneath the crowns of 87 isolated trees.

	Axis 1	Axis 2	Axis 3
Percentage of Variance Accounted for by the Explanatory Variables	5.00	3.29	2.61
P-Value	<0.001	<0.001	<0.001
Canonical Coefficients			
Site (Aromal)	−0.0853	−0.2069	0.1293
Site (Lamentos)	0.1897	−0.1915	0.0104
$Area_{100}$	0.0099	0.0428	0.0738
RhH	0.0246	−0.0405	−0.0491
N-fixation (yes)	0.0915	−0.0055	0.0687

Only the significant axes ($P < 0.05$) and the explanatory variables kept in the selected model are presented.

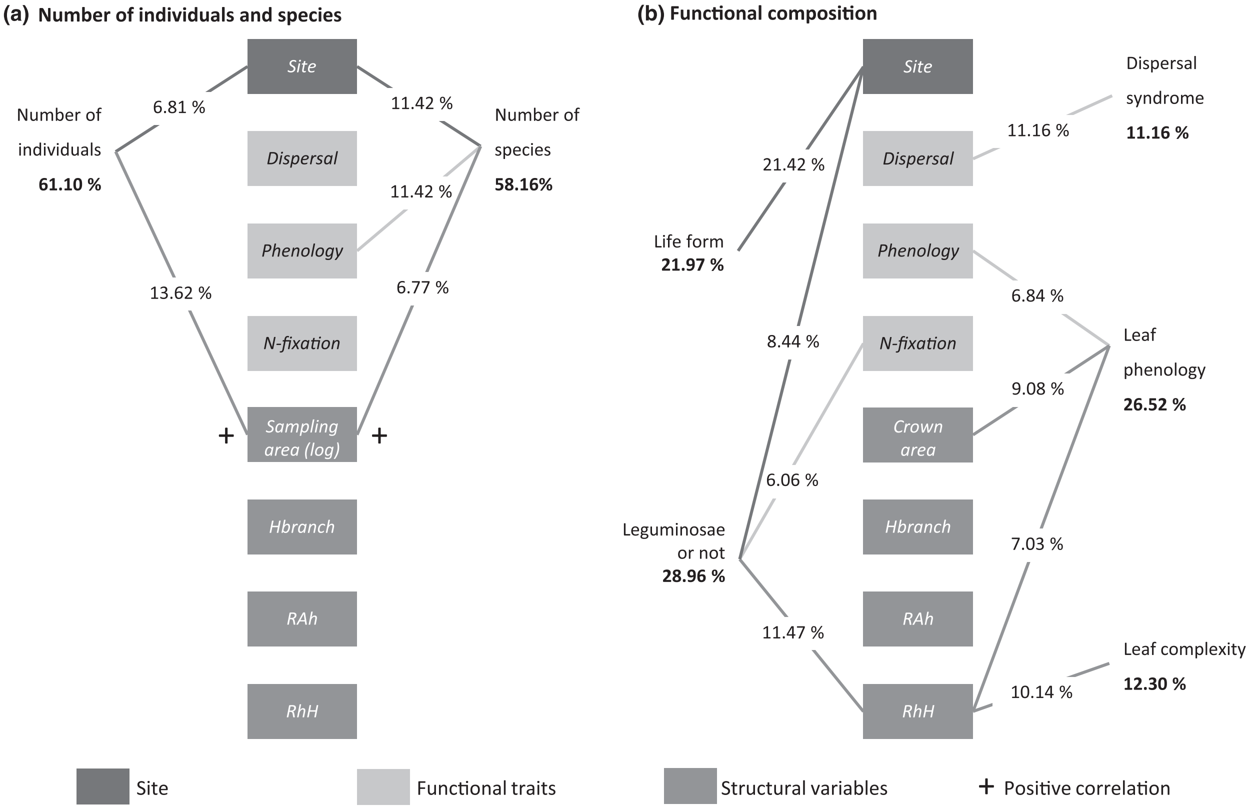

Fig. 2. Relationships between the attributes of isolated trees and the properties of the assemblages of woody plants regenerating beneath their crowns. (**a**) Number of individuals and number of species and (**b**) functional composition of the regeneration assemblage. The lines link all the significant covariates kept in the best model (attributes of isolated trees, boxes in the centre) with the response variables of this model (properties of the regeneration assemblage) on the sides. The percentage of deviance explained by each model is given in bold below each response variable, and the percentage of deviance explained by each isolated tree attribute (deviance explained by the attribute that cannot be explained by any other) in a model is given on the line. The variable *Sampling area* (log-transformed) was tested as a possible covariate only for the models of number of species and number of individuals and the variable *Crown area* only for the models of proportions of functional traits of the regeneration assemblage.

The effect of landscape factors is context-dependent

The effect of surrounding tree patches within a buffer distance on the number of individuals and species in the regeneration assemblage was observed at the smallest tested scale (100 m), for one site. This is consistent with the short distance of movement of birds and bats and the short maximum dispersal distances for anemochorous tree species in pasture. Both distances have been found to be generally <200–300 m from the forest edge (Janzen 1988; Estrada et al. 1993; Silva et al. 1996). However, in the other two sites, the number of regenerating individuals

Table 3. Results of the selected multiple GLMs between attributes of isolated trees and each of the properties of the regeneration assemblage in turn.

	Properties of Regeneration Assemblage						
	Number of Individuals	Number of Species	Prop. Trees and Shrubs	Prop. Zoochorous	Prop. Deciduous	Prop. Compound-Leaved	Prop. Leguminosae
Obs. Number	88	88	76	77	76	76	76
Explained Deviance (%)	61.10	58.16	21.97	11.16	26.52	12.30	28.96
P-Value	<0.001	<0.001	<0.001	0.002	0.002	0.006	<0.001
Coefficients							
Site Aromal	0.653**	0.522***	−0.468***	–	–	–	0.720**
Site Lamentos	−0.315 n.s.	−0.312*	−0.036 n.s.	–	–	–	0.227 n.s.
Log Sampling area	0.908***	0.404***	NA	NA	NA	NA	NA
Crown area	NA	NA	–	–	−0.001**	–	−0.002 n.s.
Hbranch	–	–	–	–	–	–	–
RhH	–	–	–	–	1.227*	2.762**	2.637*
RAh	–	–	–	–	−0.002 n.s.	–	–
Dispersal (Zoochorous)	–	–	–	0.610**	–	–	–
Phenology (Evergreen)	0.227 n.s.	0.221*	0.131 n.s.	–	−0.625*	−0.256 n.s.	−4.614 n.s.
N-fixation (Yes)	–	–	–	–	0.150 n.s.	–	−0.486*
Interaction RhH/Phenology	–	–	–	–	–	–	5.696 n.s.
Interaction RAh/Phenology	–	–	–	–	0.025 n.s.	–	–

Obs. number is number of observations, *i.e.* number of trees that have been included in the model. The *P*-value gives the significance of the whole model. *Prop.* is the 'proportion of' (*i.e.* ratio of the number of individuals with the stated trait value:total number of individuals). The proportions of deciduous, compound-leaved and Leguminosae individuals were calculated for trees and shrubs only; all other results include all regenerating individuals of tree, shrub and liana species. Coefficients for which $P < 0.05$ are highlighted. Coefficients with $P < 0.001$ are shown as ***, $P < 0.01$ as **, $P < 0.05$ as * and $P > 0.05$ as n.s. (not significant). – indicates variables that have not been kept in the selected model. NA is not applicable: the variable *Log Sampling area* was tested as a possible covariate only for the models of number of individuals and number of species and the variable *A* only for the models of functional traits of the regeneration assemblage.

was not significantly correlated with any landscape factors. This is consistent with several studies that did not observe a significant effect of distance to the nearest forest on density or richness of the regeneration assemblage (Slocum & Horvitz 2000; Duarte et al. 2010). This suggests the potential importance of other landscape factors untested in our study, such as the direction of the tree patches relative to dominant wind direction (Janzen 2002), or presence of scattered trees or live-fences acting as stepping stones and corridors for disperser birds and bats (Estrada et al. 1993; Chazdon et al. 2011). Although landscape factors are considered to mainly act on seed dispersal limitation, they could also influence environmental conditions (Pejchar et al. 2008). In our study, this latter mechanism may be the best explanation for the decrease in proportion of regenerating individuals comprising species with compound leaves when the area of tree patches within a buffer distance increased, as this trait has been shown to be associated with dry conditions (Poorter & Markesteijn 2008). Measurement of environmental conditions under isolated trees would be needed to provide direct evidence of the mechanisms by which landscape factors influence regeneration. Nonetheless, the correlations found between landscape factors and functional composition of regenerating communities indicates that the effect of landscape factors are non-neutral (Vellend et al. 2014).

In our study, the effect of site identity on the number of individuals and species in the regeneration assemblage is partly explained by the correlations between site identity and landscape factors: there were more individuals and species in the site with a higher area of tree patches in the vicinity (Fig. 1, Table 3, Appendices S3 and S4). The variable *Site* can also be considered as a proxy for non-measured variables: its effect can be attributed to differences in the composition of the local species pool, even though the sites are never more than 12 km apart. It can also reflect other factors such as past land use, current management (including the effect of cattle), variation in soils, seed predation and insect herbivory, all of which have been shown to be important in controlling the process of secondary succession (Chazdon et al. 2003).

Attributes of isolated trees influence the functional composition of regeneration assemblages

Attributes of the studied isolated trees were clearly linked to the functional composition of the regeneration assemblage beneath their crowns (Table 3, Fig. 2), while showing little influence on their taxonomic composition (Table 2). Our results suggest two mechanisms to explain this effect: amelioration of environmental conditions and attraction of seed dispersal agents.

The correlations that we found between the isolated trees' structural variables and leaf phenological habit and the regeneration assemblage's proportion of individuals having traits associated with tolerance to drought and heat (deciduous and compound leaves; Poorter & Markesteijn 2008) suggest that isolated trees affect regeneration through environmental amelioration, as found by Duarte et al. (2010). An increase in crown area is associated with the casting of more shade beneath the tree crown, and thus a greater amelioration of the air temperature (Rhoades et al. 1998), air humidity and soil moisture micro-environment (Callaway 2007). Evergreen and semi-deciduous isolated trees provide shade during the dry season and are therefore expected to mitigate high temperatures and low air humidity. While the effects of structural variables and leaf phenological habit of isolated trees are likely to interact, our results did not quite show this to be significant ($P = 0.064$ for the interaction of the ratio crown area:crown length and the phenological habit of the isolated tree in the model for regeneration assemblage leaf phenology). Mitigation of harsh environmental conditions is expected to allow individuals of species with traits generally associated with a lower tolerance of drought and heat (simple leaves and evergreen) to establish. Such positive effects of tree shade are not supported in humid tropical areas (Slocum 2001) where water limitation is not as severe as in the dry tropics.

Seed dispersal syndrome of isolated trees correlated with the proportion of individuals of species with different dispersal syndromes in the regeneration assemblage. Our model predicts almost 1.3 times as many zoochorous individuals regenerating under a zoochorous tree than under an anemochorous tree (Appendix S5). Many studies have reported a higher number of zoochorous species regenerating under isolated trees than in open pasture (Guevara et al. 1986, 1992; Galindo-González et al. 2000; Carrière et al. 2002; Zahawi & Augspurger 2006), which can be attributed to their attraction of seed dispersers, mainly birds (Silva et al. 1996; de la Peña-Domene et al. 2014) but also bats (Galindo-González et al. 2003). However, most studies do not disentangle the attraction of dispersers for perching or foraging. The link that we found between the dispersal syndrome of isolated trees and of woody individuals regenerating beneath their crowns provides good evidence of the importance of attraction for foraging by seed dispersers. Some studies have found more seeds under zoochorous trees (Slocum & Horvitz 2000; Carrière et al. 2002) but in our case, the total number of seedlings was not correlated with the seed dispersal syndrome of the tree, presumably because of the filtering effects of seed germination and seedling establishment (Howe et al. 2010).

The correlation between the proportion of Leguminosae individuals and the attributes of isolated trees (N-fixation capacity and ratio crown length:tree height) that we found supports the designation of Leguminosae as a distinct functional group in TDF with a distinct response to small-scale variation in environmental conditions relative to competing plants of non-Leguminosae species. In the same region, Powers & Tiffin (2010) found that the values of leaf C and N content, wood density and leaf stoichiometry differed significantly between Leguminosae and non-Leguminosae, reflecting differences in physiological processes. The negative correlation that we found between regeneration of Leguminosae and N-fixing capacity of isolated trees could be attributed to a loss of the competitive advantage of regenerating Leguminosae in soils of higher N status or to the local abundance of Leguminosae-specific pathogens or pests.

Although our methodological approach does not allow for a formal test of the relative importance of deterministic vs stochastic processes (Vellend et al. 2014), it is interesting that the attributes of isolated trees contribute very little to the variation in the model of taxonomic composition, while their contribution is notably greater in the models of functional composition, suggesting a stronger determinism of functional composition than taxonomic composition. Several studies of successional woody (Alvarez-Anorve et al. 2012; Muniz-Castro et al. 2012; Swenson et al. 2012; Dent et al. 2013) or grassland (Fukami et al. 2005; Purschke et al. 2013) communities provide evidence of a contrast between the predictability of functional composition and stochasticity of taxonomic and phylogenetic compositions. Whereas predictable deterministic processes shape the functional composition, the functional redundancy of species (Hubbell 2005) promotes a non-deterministic taxonomic composition, depending on a stochastic history of colonization by species in the early stages of succession and on the local species pool. Examining succession through the lens of functional composition rather than taxonomic composition can reveal the deterministic role of resource acquisition and reproduction strategies and therefore promote a better understanding of successional trajectories (Poorter et al. 2004; Lebrija-Trejos et al. 2010b).

Conclusion

Although our study is a snapshot of the early stages of secondary TDF succession, it can inform predictions of longer-term successional trajectories because the regeneration assemblages that we studied will be the origin of future stages, should the pastures be abandoned. Since we observed a correlation between the functional traits of isolated trees and the functional composition of the regeneration assemblage, the species identity of isolated trees present in the pastures is expected to have a long-term effect on the later stages of succession, as observed by Sandor & Chazdon (2014) in humid tropical forest. In other words, these later stages are dependent on the history of colonization (Fukami 2010).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Detailed methods.

Appendix S2. Abundance of species of surveyed regenerating woody plants and isolated trees per site.

Appendix S3. Characteristics of isolated trees and regenerating woody plants.

Appendix S4. Selected models for the number of individuals and the number of species in the regeneration assemblage.

Appendix S5. Selected models for functional composition of the regeneration assemblage.

Supporting information to the paper
Derroire, G. et al. Isolated trees as nuclei of regeneration in tropical pastures: testing the importance of niche-based and landscape factors. *Journal of Vegetation Science.*

Appendix S1. Detailed methods

Past and present land uses of the study sites

The sites were converted into pasture more than 45 years ago. In the three sites, pasture grasses (e.g. *Andropogon* sp.*, Bracharia* spp.) were seeded more than a decade ago and have naturally regenerated since then. The pasture sites are cleaned manually (Aromal) or using a tractor (Lamentos and Ahogados). Herbicide is also used in Ahogados and Aromal. Fire is never used as a management practice but can occur accidentally. Individual pasture sites are grazed by approximately two cows ha^{-1} (Aromal and Ahogados) or seven cows ha^{-1} (Lamentos) in a cycle of about 20 days of grazing alternating with ungrazed periods.

Attributes of isolated trees

To measure the landscape factors, the coordinates of each tree were recorded using a Global Positioning System unit (Garmin GPSMAP 62) and imported into ArcGIS (ESRI, 1999-2009) using the WGS 1984 UTM zone 16N projection. Two orthophotos were used to delimit the tree patches in, and surrounding, each site: BingMaps, image captured in July 2004 (Microsoft Corporation, 2009), and ESRI World Imagery, captured in January 2011 (Geoeye, 2011). These two orthophotos were captured during different seasons providing a contrast in vegetation leaf phenology, which improved the accuracy of patch delineation. Inclusion as a tree patch was based on a predominantly closed canopy of mature trees in an area ≥ 400 m²; this included riparian vegetation. Whenever possible, the tree patches were verified on-site. Using ArcGIS, we calculated the following landscape factors for each tree: distance to the nearest tree patch (*Distance*), and the area of tree patches in buffers of 100 m (*Area100*), 500 m (*Area500*) and 1000 m (*Area1000*) around the focal tree.

The structural variables measured for each tree were: total height (*Height*), height of the bottom of the lowest branch (*Hbranch*) (using a hypsometer), longest projected crown diameter (*D*) and its perpendicular diameter (*d*) (using a tape measure). From these, *Crown length* (= *Height - Hbranch*), *Crown area* (= π x *D* x *d* / 4), *Crown volume* (= π x *Crown length* x *D* x *d* / 6), ratio of crown length : tree height (*RhH*), ratio of crown area : tree height (*RAH*), ratio of crown volume : tree height (*RVolH*) and ratio of crown area : crown length (*RAh*) were calculated. The regenerating individuals were surveyed within the area below a vertical projection of the crown plus a one metre buffer, the sampling area, calculated as *Sampling area* = π x (*D*+2) x (*d*+2) / 4.

Properties of regeneration assemblage: categorisation of functional traits

To characterise the life-form of the regenerating woody plants, trees and shrubs were lumped in the same category because the high rate of resprouting in TDF makes the limit between these life forms hard to define and many species are described as “trees or shrubs” in the literature resources that we used. The two leaf phenological categories (evergreen and semi-deciduous *vs* fully deciduous) were designed to separate trees that retain their leaves and therefore have the potential to be photosynthetically active during at least several months of the dry season, from those that do not. Seed dispersal syndrome was also divided into two categories (zoochorous *vs* anemochorous and autochorous) to separate the species whose dispersal was liable to be influenced by the potential attraction of animal dispersers by the isolated tree, from those where this was not the case.

Statistical analysis

To test the influence of each landscape factor on the number of regenerating individuals, their number of species and their functional composition, we performed simple negative binomial and quasi-binomial GLMs to account for overdispersion. A preliminary data exploration showed collinearity between *Distance* and $Area_{100}$, between $Area_{500}$ and $Area_{1000}$ (Pearson correlation ≥ 0.7) and between *Site* and all landscape factors (p-value of Anova ≤ 0.05). Models were fitted site-by-site and for one landscape factors at a time, to avoid bias due to collinearity between covariates (Zuur et al. 2010).

The RDA was conducted on the floristic table of 87 trees (an outlier for structural variables, a tree with no regenerating plants beneath its crown, and a tree of a species with no available value for *Phenology* were excluded).

To test the respective influence of the attributes of isolated trees on the number of individuals, the number of species and the functional composition of the regeneration assemblage, we used multiple GLMs. Data exploration (Zuur et al. 2010) showed collinearity among the structural variables. This led us to consider for all models only *Hbranch*, *RAh*, and *RhH*, which presented low levels of collinearity (Pearson correlation ≤ 0.25) and low levels of clustering on the first three axes of a Principal Component Analysis. For the models of number of individuals and number of species in the regeneration assemblage, we could have scaled these variables to express them per m². However, that would have imposed a coefficient of correlation of one, which was not justified as an *a priori* assumption. We therefore used *Sampling area* as an explanatory variable and log-transformed it because we assumed that these two variables would be proportional to the sampling area. The variable *Crown area* was included in the models of functional composition for which *Log Sampling area* was not used.

For the functional traits of isolated trees, data exploration showed collinearity of *Dispersal* with *Phenology* and *N-fixation* (χ^2 p-value < 0.001). We therefore chose to include either *Dispersal* or *Phenology* and *N-fixation* in each analysis depending on the ecological hypothesis that it was testing (when neither of the two options was more relevant than the other, we fitted two candidate models and kept the better one). The interactions between *Phenology* and structural variables (*RAh* and *RhH*) were the only ones considered, because we wanted to test if a potential effect of tree structure could differ between evergreen and deciduous trees, since in TDF leaf phenology influences the effect of trees on regeneration (Derroire et al. 2016). We used negative-binomial distributions for count data (number of individuals and number of species) and quasi-binomial GLMs for proportional data (functional composition) to account for overdispersion. The log-link function was used for all negative-binomial GLMs. For quasi-binomial GLMS, the link function was cloglog for the proportion of trees and shrubs and the proportion of deciduous species, since it is better suited to these relatively unbalanced proportions (Zuur et al. 2013), and the commonly used logit function for the three other proportions. The outlier tree for structural variables was excluded from all the models and trees with fewer than ten regenerating individuals were excluded from the models of functional composition of the regeneration assemblage (because for such a low number of individuals calculating a proportion is too inaccurate). The best models were selected by performing a backward selection based on the Akaike Information Criterion (AIC) for negative-binomial GLMs and on the quasi-AIC (Burnham & Anderson 2002) for quasi-binomial GLMs. The selected models were validated by visually checking for the absence of patterns in the graphs of the residuals plotted against fitted values and covariates, and in maps of residuals according to the position of the trees. The goodness of fit of each GLM was expressed as the deviance explained by the model (Zuur et al. 2013). To obtain the deviance uniquely explained by each explanatory variable, we calculated the difference between the full model and the model fitted without this variable (keeping the dispersion parameter constant). The p-value of each whole GLM was obtained by performing a Chi-square test (for negative-binomial GLMs) or an F-test (for quasi-binomial GLMs) on the reduction of deviance of the fitted model compared with the null model.

The variables considered for each analysis are presented in Table S1-1 below.

Table S1-1. Attributes of isolated trees used in the models. Type of model refers to the model for which each variable was used: (A) influence of landscape factors on regeneration; influence of isolated tree attributes on (B) the taxonomic composition, (C) the number of individuals and species, and (D) the functional composition of the regeneration assemblage. y/n indicates models for which the variable is either included or not, depending on the modelled property of the regeneration assemblage.

Attribute of the isolated trees	Abbreviation	Type of variable	Unit/number of categories	Type of model			
				A	B	C	D
Site identity	*Site*	categorical	3	yes	yes	yes	yes
Landscape factors							
distance to nearest tree patch	*Distance*	continuous	km	yes	yes	no	no
area of tree patches in a 100 m buffer	*$Area_{100}$*	continuous	ha	yes	yes	no	no
area of tree patches in a 500 m buffer	*$Area_{500}$*	continuous	ha	yes	yes	no	no
area of tree patches in a 1000 m buffer	*$Area_{1000}$*	continuous	ha	yes	yes	no	no
Individuals structural variables							
total height	*Height*	continuous	m	no	yes	no	no
height of the lowest part of the lowest branch	*Hbranch*	continuous	m	no	yes	yes	yes
crown length	*Crown length*	continuous	m	no	yes	no	no
crown area	*Crown area*	continuous	m^2	no	yes	no	yes
crown volume	*Crown volume*	continuous	m^3	no	yes	no	no
ratio crown length : tree height	*RhH*	continuous	m/m	no	yes	yes	yes
ratio crown area : tree height	*RAH*	continuous	m^2/m	no	yes	no	no
ratio crown volume : tree height	*RVolH*	continuous	m^3/m	no	yes	no	no
ratio crown area : crown length	*RAh*	continuous	m^2/m	no	yes	yes	yes
sampling area (*A* plus a one meter buffer)	*Sampling area*	continuous	m^2	no	no	Log	no
Species functional traits							
dispersal syndrome	*Dispersal*	categorical	2	no	yes	y/n	y/n
leaf phenological habit	*Phenology*	categorical	2	no	yes	y/n	y/n
capacity to fix nitrogen	*N-fixation*	categorical	2	no	yes	y/n	y/n

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Appendix S2. Abundance of surveyed regenerating woody plants and isolated trees species per site. The number of regenerating individuals excludes individuals conspecific with the isolated tree above (and is therefore the number used in the calculation of all properties of the regeneration assemblage except the rate of conspecificity). Among the 46 families, Leguminosae had the highest relative density of regenerating individuals (44.4%, with 30.3% being Mimosoideae) and Leguminosae also dominated in terms of number of species accounting for 20.8%, with 8.8% being Papilionoideae and 8% Mimosoideae. Bignoniaceae contributed 9.6% of the species and Rubiaceae 7.2%. While Leguminosae dominated the number of individuals of tree and shrub species (48.67%), Bignoniaceae dominated the lianas (44.7%).
Nomenclature follows The Plant List (http://www.theplantlist.org/; accessed on 15 Jan 2015).

			Number of surveyed regenerating individuals			Number of surveyed isolated trees		
Species	Familly	Life form	Ahogados	Aromal	Lamentos	Ahogados	Aromal	Lamentos
Acacia collinsii	Leguminosae	Tree/shrub	324	616	83	-	-	-
Acacia farnesiana	Leguminosae	Tree/shrub	-	11	70	-	-	-
Acacia tenuifolia	Leguminosae	Woody liana	-	17	-	-	-	-
Aegiphila panamensis	Lamiaceae	Tree/shrub	-	5	-	-	-	-
Aeschynomene brasiliana	Leguminosae	Tree/shrub	-	1	-	-	-	-
Agonandra macrocarpa	Opiliaceae	Tree/shrub	-	2	-	-	-	-
Albizia adinocephala	Leguminosae	Tree/shrub	-	7	-	-	-	-
Albizia guachapele	Leguminosae	Tree/shrub	-	5	-	-	-	-
Albizia niopoides	Leguminosae	Tree/shrub	-	2	-	-	-	-
Albizia saman	Leguminosae	Tree/shrub	-	12	-	-	1	-
Alibertia edulis	Rubiaceae	Tree/shrub	18	1	1	-	-	-
Allophylus racemosus	Sapindaceae	Tree/shrub	-	2	-	-	-	-
Amphilophium crucigerum	Bignoniaceae	Woody liana	-	7	-	-	-	-
Amphilophium paniculatum	Bignoniaceae	Woody liana	-	73	7	-	-	-
Andira inermis	Leguminosae	Tree/shrub	-	-	-	1	2	-
Anemopaegma orbiculatum	Bignoniaceae	Woody liana	-	22	-	-	-	-
Annona holosericea	Annonaceae	Tree/shrub	1	-	-	-	-	-
Annona reticulata	Annonaceae	Tree/shrub	1	54	8	-	-	-
Ardisia revoluta	Primulaceae	Tree/shrub	1	1	-	-	-	-
Banisteriopsis muricata	Malpighiaceae	Woody liana	2	55	2	-	-	-
Bauhinia ungulata	Leguminosae	Tree/shrub	-	192	2	-	-	-
Bignonia aequinoctialis	Bignoniaceae	Woody liana	2	39	-	-	-	-
Bignonia diversifolia	Bignoniaceae	Woody liana	6	101	-	-	-	-
Bixa orellana	Bixaceae	Tree/shrub	-	31	-	-	-	-
Bonellia nervosa	Primulaceae	Tree/shrub	29	36	10	-	-	-
Bronwenia cornifolia	Malpighiaceae	Woody liana	8	50	-	-	-	-
Bursera simaruba	Burseraceae	Tree/shrub	41	334	42	-	-	-
Bursera tomentosa	Burseraceae	Tree/shrub	2	-	1	-	-	-
Byrsonima crassifolia	Malpighiaceae	Tree/shrub	-	1	3	-	-	13
Calliandra calothyrsus	Leguminosae	Tree/shrub	-	6	-	-	-	-
Calycophyllum candidissimum	Rubiaceae	Tree/shrub	-	2	-	-	-	-
Canavalia brasiliensis	Leguminosae	Woody liana	-	2	-	-	-	-
Cascabela ovata	Apocynaceae	Tree/shrub	-	1	-	-	-	-
Casearia arguta	Salicaceae	Tree/shrub	3	-	-	-	-	-
Casearia corymbosa	Salicaceae	Tree/shrub	-	2	-	-	-	-
Casearia nitida	Salicaceae	Tree/shrub	15	133	1	-	-	-
Casearia sylvestris	Salicaceae	Tree/shrub	-	13	2	-	-	-
Cassia grandis	Leguminosae	Tree/shrub	-	1	-	-	1	-
Cecropia peltata	Urticaceae	Tree/shrub	-	1	-	-	-	-
Cedrela odorata	Meliaceae	Tree/shrub	-	9	-	-	1	-
Chomelia spinosa	Rubiaceae	Tree/shrub	9	19	4	-	-	-
Coccoloba venosa	Polygonaceae	Tree/shrub	-	1	-	-	-	-
Cochlospermum vitifolium	Bixaceae	Tree/shrub	2	228	17	-	-	-
Combretum farinosum	Combretaceae	Woody liana	1	116	-	-	-	-
Cordia alliodora	Boraginaceae	Tree/shrub	1	25	2	-	-	1
Cordia guanacastensis	Boraginaceae	Tree/shrub	48	87	55	-	-	-
Cordia inermis	Boraginaceae	Tree/shrub	-	37	29	-	-	-
Cordia panamensis	Boraginaceae	Tree/shrub	-	20	-	-	-	-
Crescentia alata	Bignoniaceae	Tree/shrub	1	56	9	2	2	-
Croton niveus	Euphorbiaceae	Tree/shrub	-	1	-	-	-	-
Croton schiedeanus	Euphorbiaceae	Tree/shrub	-	-	1	-	-	-

Cupania guatemalensis	Sapindaceae	Tree/shrub	-	2	-	-	-	-
Curatella americana	Dilleniaceae	Tree/shrub	-	-	-	1	-	-
Cydista heterophylla	Bignoniaceae	Woody liana	-	10	-	-	-	-
Dalbergia retusa	Leguminosae	Tree/shrub	-	1	-	6	-	-
Diospyros salicifolia	Ebenaceae	Tree/shrub	23	11	10	-	-	-
Diphysa americana	Leguminosae	Tree/shrub	-	5	-	-	1	-
Enterolobium cyclocarpum	Leguminosae	Tree/shrub	63	568	32	-	1	-
Erythroxylum havanense	Erythroxylaceae	Tree/shrub	2	-	-	-	-	-
Eugenia salamensis	Myrtaceae	Tree/shrub	1	4	-	1	-	-
Ficus cotinifolia	Moraceae	Tree/shrub	1	-	-	1	-	-
Ficus cotinifolia var. hondurensis	Moraceae	Tree/shrub	2	-	-	-	-	-
Ficus crocata	Moraceae	Tree/shrub	-	-	-	1	-	-
Forsteronia spicata	Apocynaceae	Woody liana	11	18	-	-	-	-
Genipa americana	Rubiaceae	Tree/shrub	68	8	3	3	-	-
Gliricidia sepium	Leguminosae	Tree/shrub	1	120	-	-	4	3
Godmania aesculifolia	Bignoniaceae	Tree/shrub	-	-	-	-	-	1
Guazuma ulmifolia	Malvaceae	Tree/shrub	79	245	21	3	5	12
Hamelia patens	Rubiaceae	Tree/shrub	-	7	-	-	-	-
Handroanthus impetiginosus	Bignoniaceae	Tree/shrub	-	7	-	-	-	-
Helicteres guazumifolia	Malvaceae	Tree/shrub	14	4	6	-	-	-
Hiraea reclinata	Malpighiaceae	Woody liana	-	1	-	-	-	-
Hymenaea courbaril	Leguminosae	Tree/shrub	-	-	-	-	1	-
Jatropha curcas	Euphorbiaceae	Tree/shrub	-	-	2	-	-	-
Karwinskia calderonii	Rhamnaceae	Tree/shrub	-	2	-	1	-	-
Licania arborea	Chrysobalanaceae	Tree/shrub	1	5	-	1	1	-
Lonchocarpus felipei	Leguminosae	Tree/shrub	-	11	-	-	1	-
Lonchocarpus minimiflorus	Leguminosae	Tree/shrub	-	29	-	-	-	-
Lonchocarpus oliganthus	Leguminosae	Tree/shrub	-	2	1	-	-	-
Lonchocarpus rugosus	Leguminosae	Tree/shrub	-	5	-	-	2	-
Luehea candida	Malvaceae	Tree/shrub	-	7	-	-	-	-
Machaerium biovulatum	Leguminosae	Tree/shrub	-	12	-	-	-	-
Machaerium salvadorense	Leguminosae	Woody liana	-	1	-	-	-	-
Maclura tinctoria	Moraceae	Tree/shrub	-	1	1	-	3	-
Malpighia glabra	Malpighiaceae	Tree/shrub	-	4	-	-	-	-
Manilkara chicle	Sapotaceae	Tree/shrub	1	-	-	2	1	-
Mansoa hymenaea	Bignoniaceae	Woody liana	-	15	-	-	-	-
Margaritaria nobilis	Phyllanthaceae	Tree/shrub	-	19	1	-	-	-
Marsdenia engleriana	Apocynaceae	Woody liana	-	1	-	-	-	-
Myrospermum frutescens	Leguminosae	Tree/shrub	-	28	-	-	-	-
Pachira quinata	Malvaceae	Tree/shrub	-	52	-	3	2	-
Paullinia cururu	Sapindaceae	Woody liana	8	2	-	-	-	-
Piper auritum	Piperaceae	Tree/shrub	-	1	-	-	-	-
Piper tuberculatum	Piperaceae	Tree/shrub	-	1	-	-	-	-
Piscidia carthagenensis	Leguminosae	Tree/shrub	-	14	-	-	-	-
Pisonia macranthocarpa	Nyctaginaceae	Tree/shrub	1	32	-	-	-	-
Pithecellobium lanceolatum	Leguminosae	Tree/shrub	-	1	-	-	-	-
Platymiscium pleiostachyum	Leguminosae	Tree/shrub	-	1	-	-	-	-
Psidium guajava	Myrtaceae	Tree/shrub	36	-	1	-	-	-
Psychotria carthagenensis	Rubiaceae	Tree/shrub	3	11	1	-	-	-
Psychotria panamensis	Rubiaceae	Tree/shrub	-	3	-	-	-	-
Pterocarpus michelianus	Leguminosae	Tree/shrub	-	1	-	-	-	-
Randia monantha	Rubiaceae	Tree/shrub	1	3	-	-	-	-
Randia thurberi	Rubiaceae	Tree/shrub	18	1	-	-	-	-
Rauvolfia tetraphylla	Apocynaceae	Tree/shrub	29	49	4	-	-	-
Roupala montana	Proteaceae	Tree/shrub	1	-	-	-	-	-
Sapranthus palanga	Annonaceae	Tree/shrub	-	8	-	-	-	-
Semialarium mexicanum	Celastraceae	Tree/shrub	143	60	2	-	-	-
Senna atomaria	Leguminosae	Tree/shrub	-	2	6	-	-	-
Senna pallida	Leguminosae	Tree/shrub	281	151	109	-	-	-
Senna papillosa	Leguminosae	Tree/shrub	-	4	-	-	-	-
Serjania schiedeana	Sapindaceae	Woody liana	23	13	10	-	-	-

Simarouba amara	Simaroubaceae	Tree/shrub	1	30	-	-	-	-
Solanum hazenii	Solanaceae	Tree/shrub	-	1	-	-	-	-
Spondias mombin	Anacardiaceae	Tree/shrub	1	19	5	-	-	-
Spondias purpurea	Anacardiaceae	Tree/shrub	-	4	-	-	-	-
Stemmadenia obovata	Apocynaceae	Tree/shrub	13	37	10	-	-	-
Swietenia macrophylla	Meliaceae	Tree/shrub	-	-	-	1	-	-
Tabebuia ochracea	Bignoniaceae	Tree/shrub	-	105	-	-	-	-
Tabebuia rosea	Bignoniaceae	Tree/shrub	2	3	1	1	-	-
Tetracera volubilis	Dilleniaceae	Woody liana	3	-	1	-	-	-
Thouinidium decandrum	Sapindaceae	Tree/shrub	1	35	-	-	1	-
Trichilia americana	Meliaceae	Tree/shrub	18	22	3	-	-	-
Trichilia glabra	Meliaceae	Tree/shrub	1	-	-	-	-	-
Trichilia havanensis	Meliaceae	Tree/shrub	1	40	-	-	-	-
Trigonia rugosa	Trigoniaceae	Woody liana	-	2	2	-	-	-
unknown 1	NA	Tree/shrub	-	3	-	-	-	-
Varronia macrocephala	Boraginaceae	Tree/shrub	-	-	1	-	-	-
Xylosma flexuosa	Salicaceae	Tree/shrub	-	1	9	-	-	-
Zapoteca mollis	Leguminosae	Tree/shrub	-	2	-	-	-	-
Zuelania guidonia	Salicaceae	Tree/shrub	-	-	-	2	-	-
			1367	**4304**	**591**	**30**	**30**	**30**

Appendix S3. Characteristics of isolated trees and regenerating woody plants

Characteristics of isolated trees

The 90 isolated trees represented 30 species from 18 families (Appendix S2); Malvaceae and Leguminosae were the most abundant. *Height* ranged from 3.5 to 22 m (mean 10.1 m, excluding the outlier (40 m)) and *Crown area* from 19.4 to 490.1 m² (mean 139.3 m², excluding the outlier (829.4 m²)). *Distance* ranged from 5.6 m to 189.5 m, $Area_{100}$ from 0 to 1.6 ha, $Area_{500}$ from 8.9 to 41.5 ha and $Area_{1000}$ from 64.2 to 223.1 ha. Of the isolated trees, 68.9% were zoochorous, 35.9% evergreen or semi-deciduous and 24.4% N-fixing. Table S3-1. below summarises the characteristics of the communities of isolated trees studied in each site.

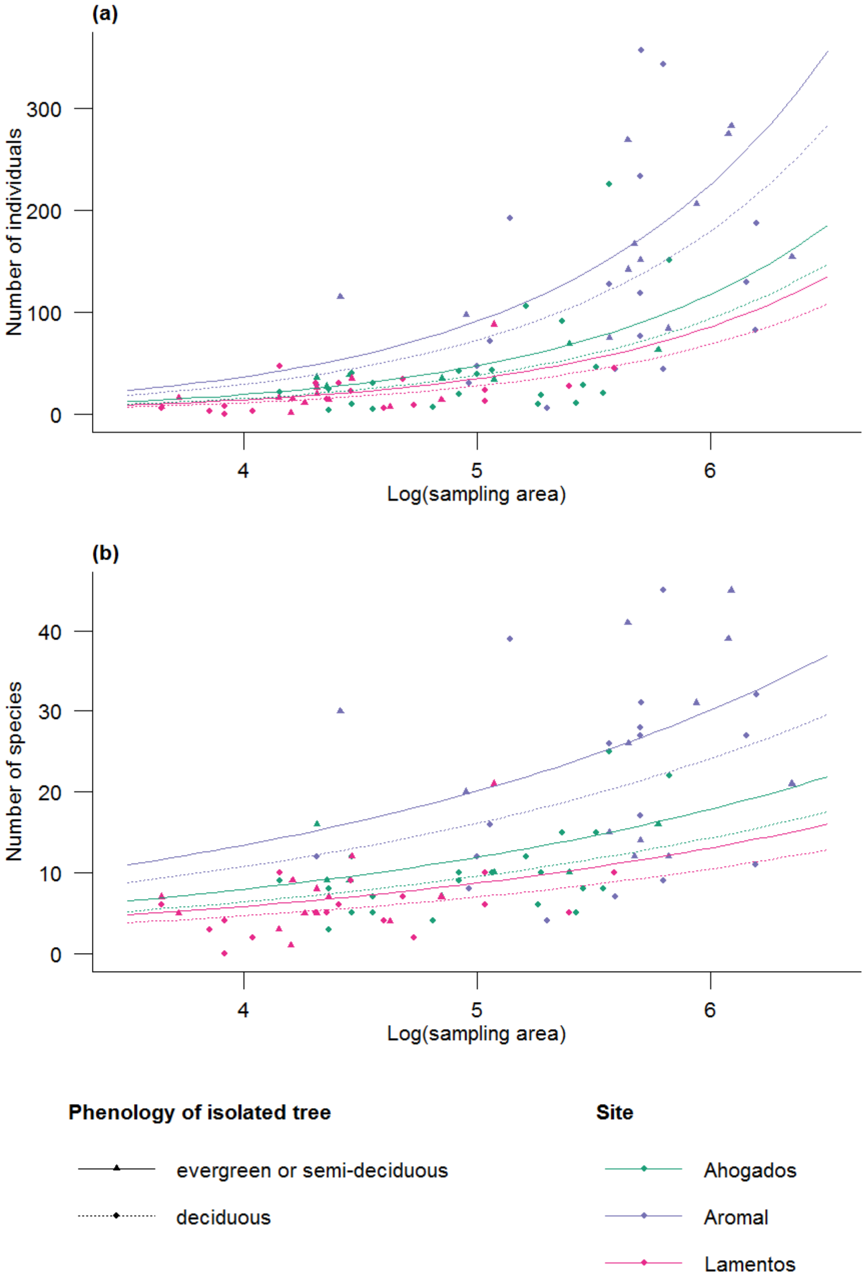
Characteristics of regenerating woody plants

We surveyed regeneration of woody plant species in a total of 17 089 m² and recorded 6802 individuals (90.7% tree and shrub species; 9.3% of lianas), including individuals conspecific with the isolated tree above. The number of regenerating individuals beneath the crown of each isolated tree ranged from 0 to 392 (415 for the outlier tree). Among the 126 regenerating woody species from 46 families (Appendix S2), the most abundant trees and shrubs were *Acacia collinsii* and *Enterolobium cyclocarpum* (both zoochorous and deciduous Leguminosae with compound leaves), and of woody lianas were *Combretum farinosum*, *Cydista diversifolia* and *Amphilophium paniculatum* (all anemochorous). Zoochory was the dominant type of seed dispersal accounting for 62.0% of the regenerating individuals (54.4% of the species) and from the information provided in our data sources was mainly attributable to birds and to a lesser extent bats and other mammals. Among regenerating plants of tree and shrub species, deciduous was the dominant type of phenology (91.2% of individuals and 63.8% of species), whereas there was a closer balance between the two leaf types with 57.5% of regenerating individuals and 44.8% of species having compound leaves. The great majority of species in the regeneration assemblage (87.8% for Lamentos, 83.7% for Aromal and 80.0% for Ahogados) were not represented by any isolated tree studied in that site.

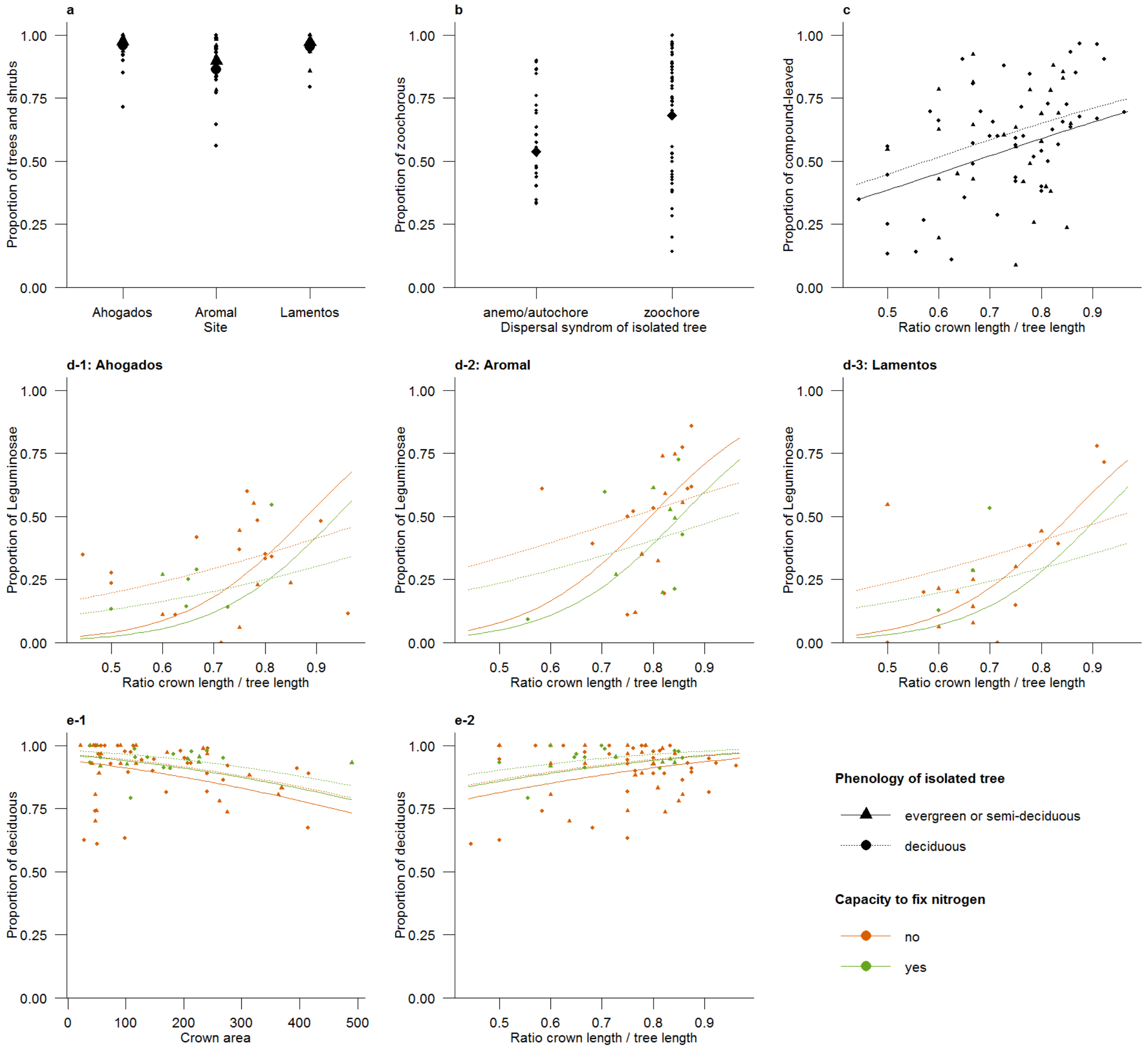
Table S3-1. Characteristics of the communities of isolated trees sampled in each site. The listed main species are those with at least two individuals among the trees sampled in that site; they are ordered by abundance. Nomenclature follows The Plant List (http://www.theplantlist.org/; accessed on 15 Jan 2015).

Site	Number of species	Simpson evenness	Main species	Mean *Distance* (km)	Mean $Area_{100}$ (ha)	Mean $Area_{500}$ (ha)	Mean $Area_{1000}$ (ha)
Ahogados	16	0.67	*Dalbergia retusa* *Genipa americana* *Guazuma ulmifolia* *Pachira quinata* *Crescentia alata* *Manilkara chicle* *Zuelania guidonia*	0.079	0.23	18.65	91.05
Aromal	17	0.70	*Guazuma ulmifolia* *Gliricidia sepium* *Andira inermis* *Crescentia alata*	0.070	0.37	32.47	189.27
Lamentos	5	0.56	*Byrsonima crassifolia* *Guazuma ulmifolia* *Gliricidia sepium*	0.047	0.58	26.93	131.04
All sites	30	0.35		0.065	0.39	26.02	137.12

Appendix S4. Selected models for (a) the number of individuals (61.10% of deviance explained) (b) and the number of species (58.16% of deviance explained) if the regeneration assemblage. The models (Table 3) were selected using AIC. The points are the observed values.



Appendix S5. Selected models for functional composition of the regeneration assemblage. Selected models for the proportion of individuals in the regeneration assemblage of (a) tree and shrub species (21.97% of deviance explained by the whole model), (b) zoochorous species (11.16% of deviance explained), (c) compound-leaved species (12.30% of deviance explained), (d) Leguminosae species (28.96% of deviance explained, model presented in d1-3) and (e) deciduous species (26.52% of deviance explained, model presented in e1-2). The models (Table 3) were selected using AIC. For a and b, the small points are the observed values and the large ones are the modelled values.



Paper IV

Derroire, G., Powers, J.S., Hulshof, C.M., Cárdenas Valera, L.E, Healey, J.H. Functional strategies change through species turnover and intraspecific variation in tropical dry forest succession (manuscript under review).

Functional strategies change through species turnover and intraspecific variation in tropical dry forest succession

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Abstract

Community functional trait values, and thus plant strategies, change during forest succession in response to changing environmental conditions. This process is complex in tropical dry forests because water and light availability change in opposite directions; thus the consequences for community assembly are insufficiently understood. Moreover, we do not know the extent and direction of intraspecific variation in response to changes in environmental conditions during succession and through ontogeny. Our study aimed to understand the change in functional composition of sapling communities during succession in tropical dry forests. We asked: (1) How do plant strategies change during succession and what are the underlying environmental drivers? (2) What is the relative contribution of species turnover and intraspecific variation to functional changes during succession? (3) What is the direction of change in leaf traits with sapling ontogeny and does it correspond to that occurring during succession? We measured 15 morphological, chemical, and phenological traits on more than 800 individual saplings, and environmental variables along two successional chronosequences in Costa Rica. We found that community functional composition shifts from conservative towards acquisitive strategies during succession, underscoring the importance of changing environmental conditions for leaf resource economics. We also observed a decrease in traits associated with drought survival. Intraspecific variation of traits contributed to these changes, although less than species turnover in most cases, suggesting the importance of plastic responses within species, especially for specific leaf area. For most traits, species turnover and intraspecific variation changed in the same direction. Last, we found directional intraspecific changes with ontogeny for five traits, however their values switched from acquisitive to conservative strategies with increasing tree height. Our study highlights the importance of taking into account intraspecific variation of leaf functional traits to understand community assembly along successional gradients and the need for studies on the response of plant traits to environmental gradients for different ontogenic stages.

Keywords: Costa Rica, drought, environmental gradients, leaf functional traits, ontogenic niche shift, phenotypic plasticity, specific leaf area, regeneration niche, secondary succession, trait-environment relationship, tropical forest

Introduction

Functional traits are valuable for understanding the fitness of individual plants and the assembly of communities along environmental gradients (Reich 2014). General patterns of correlations and trade-offs among plant functional traits allow suites of correlated traits to be interpreted as plant ecological strategies (Reich 2014). Wright et al. (2004) showed that leaf functional trait values are structured along a main global axis of plant strategies: the leaf economics spectrum. At one end of this spectrum are productive strategies with a fast return on investment of resources in leaves characterized by high specific leaf area, leaf nutrient concentrations, high metabolic rates and short leaf lifespan, also called acquisitive strategies (Reich 2014). At the other end, conservative strategies, with a slow return on investment, are characterized by low metabolic rates, and expensive leaf construction and defense costs allowing a longer leaf lifespan. This spectrum is associated with resource gradients (light, water, nutrients); acquisitive strategies being advantageous in high resource environments and conservative strategies enhancing survival in low resource environments (Reich 2014).

The changes in environmental conditions during forest succession predict a change of community trait values. In tropical wet forests, the decrease of light availability leads to a change from acquisitive to conservative strategies during succession (Lohbeck et al. 2013, Lohbeck et al. 2015). However, in tropical dry forests (TDF), the high light environment of the early stages of succession combined with seasonal water limitation leads to high evaporative demand and risk of desiccation (Lebrija-Trejos et al. 2011). Under such environmental conditions, the high drought tolerance of conservative species can be advantageous (Reich 2014), predicting a trend from conservative to acquisitive strategies with succession in TDF. This hypothesis has received mixed support from field studies: for example, some studies found an increase in specific leaf area with succession (Becknell and Powers 2014, Buzzard et al. 2015), while other studies found a decrease (Lohbeck et al. 2013) or no trend (Lebrija-Trejos et al. 2010). Moreover, Lohbeck et al. (2015) and Lebrija-Trejos et al. (2010) found that leaf phenological habit and morphological traits allowing leaf cooling and water status control are more important in explaining changes in community functional composition during succession than are leaf economics strategies.

Changes in community trait values along gradients result from a combination of species turnover and changes in trait values within species (intraspecific variation, ITV) (Lepš et al. 2011). However, most studies are based on mean values per species, therefore overlooking ITV (Violle et al. 2012). Yet there is increasing evidence that ITV is not negligible compared with differences in trait values between species (Siefert et al. 2015), including in tropical forests (Hulshof and Swenson 2010, Messier et al. 2010). Moreover, ITV can represent an important part of the response of communities to environmental gradients (Lepš et al. 2011, Carlucci et al. 2015) and may even change in an opposite direction to that resulting from species turnover (Kichenin et al. 2013). The inclusion of ITV in community studies and the assessment of its contribution and direction of change relative to species turnover are therefore crucial for understanding the drivers of change in community trait values (Carlucci et al. 2015, Siefert et al. 2015).

Intraspecific trait variation can result from both genetic variation between individuals and phenotypic variation of the same genotype (Violle et al. 2012). The latter can occur in response to environmental conditions (phenotypic plasticity, Violle et al. 2012). Genetic variability and phenotypic plasticity are difficult to disentangle without experiments, but doing so is not essential for community studies because both can be linked to environmental conditions (Violle et al. 2012). Phenotypic variation can also occur during plant development (ontogeny). A decrease with ontogeny in the value of traits associated with acquisitive strategies has been observed in temperate (Thomas and Winner 2002, Niklas and Cobb 2008, Sendall and Reich 2013, Spasojevic et al. 2014) and tropical moist forests (Poorter 2007) but, to the best of our knowledge, this has not yet been studied in TDF. Because a tree growing in a successional forest may experience trait variation as a result of both changing environmental conditions and ontogeny, it is important to assess if the changes resulting from these two mechanisms show the same or opposite trends and hence reinforce or oppose each other.

Our study aims to improve understanding of the direction and drivers of change in the functional composition of sapling communities during succession in TDF. We expand on previous studies by measuring leaf traits on a large sample of leaves allowing us to assess the relative contributions of ITV and species turnover. We focus on early ontogenic stages that are particularly important for understanding species' distributions and community assembly (Poorter 2007) while still considering changes in trait values during a large ontogenic window within the sapling stage. To get a better understanding of the factors underpinning the functional changes during succession, and their generality, we measured key environmental variables and studied two different successional forests types. We asked the following questions: (1) How do plant strategies in sapling communities change during succession and what are the environmental variables driving these changes? We expected a trend from conservative to acquisitive strategies driven by a decrease in canopy openness and temperature. (2) What is the relative contribution of species turnover and ITV to the change in community leaf trait values during succession? We expected trait values to vary in a similar direction through ITV and species turnover, and ITV to have a lower but still substantial contribution. (3) What is the direction of change in leaf traits with sapling ontogeny and does it correspond to that occurring during succession? We had no *a priori* basis on which to predict the trend in trait values with ontogeny during TDF succession.

Methods

Study area and chronosequences

The study was conducted in Sector Santa Rosa (10.84° N, 85.62° W) within *Area de Conservación Guanacaste*, Costa Rica. The mean annual rainfall is 1765 mm (30 years average, Becknell and Powers 2014), with a strongly seasonal distribution (the December to mid-May dry season has little or no rain) and high inter-annual variation. The vegetation type is TDF (Holdridge et al. 1971), mostly secondary forests on land previously used for crop and cattle farming (Calvo-Alvarado et al. 2009). The past land uses are described by Powers et al. (2009). We collected data from 12 plots (each 20 x 50 m) forming two chronosequences: six plots were in forests dominated by oaks (*Quercus oleoides* Schltdl. & Cham.) (SROAK) while the other six had a more even mixture of species (SRTDF) (we use 'forest type' to refer to these two groups of plots) (Powers et al. 2009). Besides having a distinct tree composition, these two forest types are located on different soils: the oak plots are on nutrient-poor soil on volcanic pumice and the mixed-species plots are on clayey volcanic soils (Powers et al. 2009). The two forest types therefore have distinct soil chemical properties (Powers et al. 2009) and soil fungal communities (Waring et al. 2016).

Sampling design and trait measurements

We identified all saplings (1-4 m high and less than 7 cm diameter at breast height, DBH) of tree species in a 5 x 50 m plot located along the center line of each of the 20 x 50 m plots (henceforth, 'plot' refers to the 5 x 50 m area). All sampled saplings were assigned to height classes of 50 cm intervals using a graduated stick, their crown illumination index (Clark and Clark 1992) assessed visually and in June and July 2014 their leaf traits were measured.

We measured the following leaf traits associated with (1) resource economics strategies: high specific leaf area (SLA), nitrogen (LNC) and phosphorus (LPC) concentrations, leaf area (LA) and petiole length for acquisitive strategies, and high leaf thickness, leaf density, leaf dry matter content (LDMC) and leaf carbon concentration (LCC) for conservative strategies (Wright et al. 2004, Poorter 2009, Lohbeck et al. 2015), (2) tolerance of dry and hot conditions: leaf compoundness (three classes), leaf pubescence (binary), leaf phenological habit (3 classes), leaf density and LDMC (Poorter and Markesteijn 2008, Lebrija-Trejos et al. 2010, Reich 2014). We also measured (3) the stoichiometric ratios C/N and N/P because of their links to both resource acquisition strategies and nutrient limitation (Poorter 2009, Powers and Tiffin 2010), and (4) membership of the Fabaceae (legumes) because their low water usage and their capacity to fix nitrogen suggest that they can be considered as a distinct functional group (Powers and Tiffin 2010, Reyes-Garcia et al. 2012). Standard protocols were used to make these measurements (see Appendix A).

To fully take into account ITV, we measured traits on all saplings in the plots, with the exception of cases when the number of saplings per height class, per species and per plot exceeded six (6.5% of saplings were not measured for this reason; the measured saplings were chosen randomly). In a few cases (5.6% of leaves), the absence of a sufficient number of leaves prevented measurement. For calculation of community scale values, non-measured leaf trait values were extrapolated by taking the mean values for the leaves of, by order of priority, (1) the same individual (when less than three leaves could be sampled), (2) all individuals of the same species, height class and plot, (3) all individuals of the same species and plot. If none of the extrapolations were possible, values were considered missing (0.5% of leaves).

Measurements of environmental factors

The successional age of each plot (*i.e.* age since the beginning of succession) was obtained from the estimates of Powers et al. (2009), which were based on satellite images, assessment of tree age, local knowledge and stable isotopic composition of soil carbon. The basal area of each plot was calculated from the DBH of all trees ≥ 10 cm measured in 2014 by Becknell and Powers (2014). For each plot, during the wet and the dry season of 2014 we measured a set of microclimatic factors that were expected to change with the development of canopy cover occurring during secondary succession: mean air diurnal temperature (referred to as ‘air temperature’), canopy openness and soil moisture (methods described in Appendix A). Data on soil physical and chemical factors reported in Powers et al. (2009) were used as they were assumed to reflect underlying variation in parent material and weathering status among plots, and not changes with vegetation succession.

Statistical analysis

All statistical analyses were performed in R 3.2.2 (R core team 2015) using the packages ADE4 (Dray and Dufour 2007) and NLME (Pinheiro and Bates 2015).

At the community level, we combined two approaches to understand changes of trait values with succession: a multi-trait approach to understand strategies and trade-offs, and a single-trait approach because the multi-trait approach can hide changes of traits in opposite directions. For the multi-trait approach, we used the RLQ method on all traits and environmental factors (all microclimatic factors, successional age, forest type, basal area, and soil pH and clay concentration). Briefly, RLQ analysis is a multivariate technique that estimates trait-environment relationships by finding axes that maximize the squared cross-covariance of linear combinations of environmental factors and traits (Dray et al. 2014). The resulting coefficients obtained for each variable (traits and environmental factors) are used to represent the trait-environment relationship graphically. The analysis also gives the relative contribution of each trait and each environmental variable to each axis. Performing two partial RLQs (Wesuls et al. 2012) (959 individuals, 69 species) allowed separation of the ITV and species turnover components of the trait-environment relationships.

For the single-trait approach, we used the method proposed by Lepš et al. (2011) to separate the response of community trait values to environmental factors due to species turnover from that due to ITV. For each trait and each plot, we calculated two types of community weighted mean values (a) using a mean trait value *per species* and *per plot* (specific mean): changes of this value between plots reflect the effect of both species turnover and ITV and (b) using a mean trait value *per species* calculated *across plots* of the same forest type (fixed mean): changes of this value between plots are only due to species turnover. (c) The difference between these two means (specific – fixed) gives the part that is only due to ITV. For each trait and each environmental factor, we fitted a linear regression for each of these three values. This gives the slope and significance of the relationship between the environmental factors and the changes in community trait value due to (b) species turnover only and (c) ITV only, respectively. We then expressed the explained sum of squares (SS) of regression (b) (and of (c)) as a percentage of the total SS of regression (a) to get the contribution of the relationship between the environmental factor and the community trait value that is only due to species turnover (and only due to ITV) to the total variation of community trait values between plots. The contribution of the covariation between ITV and species turnover is obtained by expressing SS(a)-SS(b)-SS(c) as a percentage of the total SS and is positive if the parts due to species turnover and ITV vary in the same direction, negative otherwise. These analyses were conducted for each forest type separately. We used the *trait.flex.anova* function coded by Lepš et al. (2011). We considered only the most relevant environmental factors: successional age of the plots, air temperature and soil moisture measured during the dry season because we expected high temperature and low soil moisture availability to be limiting factors during this season, and canopy openness measured during the wet season because we expected low light to be a limiting factor during this season, soil pH because it correlates well with other variables of soil fertility (Becknell and Powers 2014), and clay concentration because it affects soil water storage.

Categorical traits did not, or very marginally, vary within species, either because the trait is inherent to the species (legumes or not), because the method of data collection only considered a single value per species (phenological habit) or because the recorded values varied very little within species (leaf compoundness and pubescence). To assess correlation between the community values for these traits and each environmental factor, we used quasi-binomial generalized linear models (GLM) to account for over-dispersion, with the proportion of individuals within a given category of a trait as a response variable. For the environmental variables of successional age, air temperature (dry season) and soil pH, we included both the environmental variable and forest type as explanatory variables in the same model. Canopy openness (wet season), soil moisture (dry season) and clay concentration were collinear with forest type so we fitted a model by forest type for these factors to avoid bias.

To test for intraspecific trait changes with the ontogenic stage of individual saplings, we used the ratio between the height of the individual and the maximum height of the species (H/Hmax) as a proxy for ontogeny, to account for differences in maximum height between species. Height was taken as the middle of the measured 50 cm height class, and Hmax was calculated from the height of the five tallest trees encountered in 60 plots in the same region (Powers et al. 2009). For each trait, we fitted linear mixed models with H/Hmax, forest type and their interaction as fixed factors, species as a random factor and the log-transformed mean values of each trait per individual as response variables. Only species for which we had Hmax and at least one individual sapling in two different height classes of the same forest type were included (420 individuals, 26 species). We used the Akaike information criterion (AIC) to select the structure of the random part of the model and the variables kept in the fixed part.

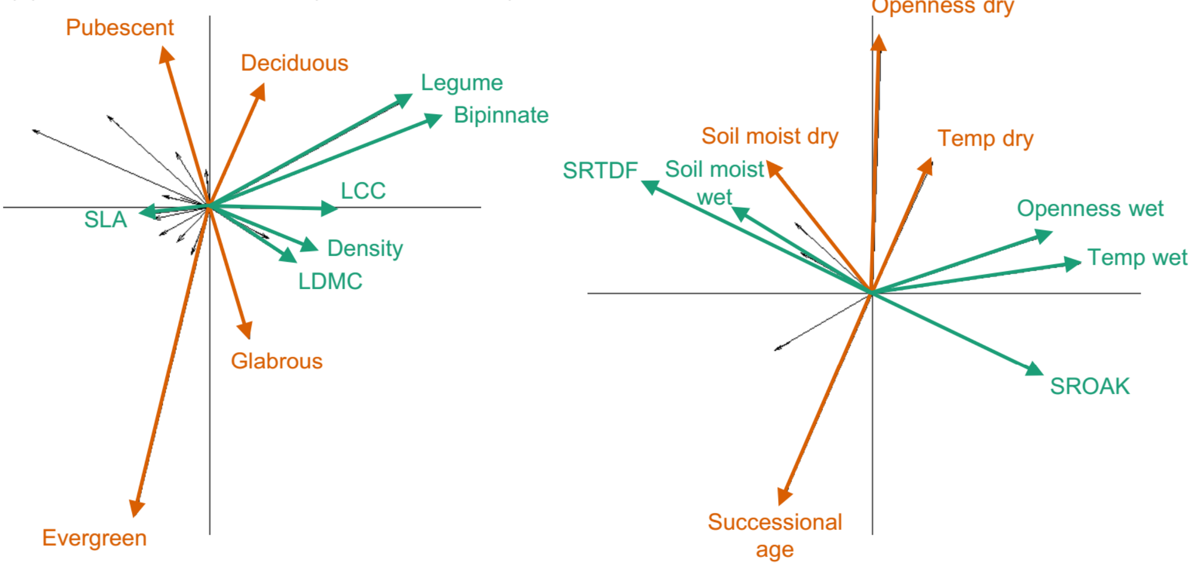
Results

We surveyed 967 saplings and measured a total of 2539 leaves on 852 saplings of 69 species. The most common families were Fabaceae and Rubiaceae (respectively 21.0% and 13.4% of individuals) and species was *Acacia collinsii* Saff. (15.9% of individuals). All species and mean trait values are listed in Appendix B. Among the environmental factors, canopy openness decreased significantly with succession, in both seasons for SROAK and in the dry season for SRTDF. Air temperature, during the dry season for SRTDF and the wet season for SROAK, tended to decrease with succession (Appendix C). Soil factors were generally not significantly correlated with successional age, which limits the risk of attributing to succession an effect actually due to soil. SRTDF plots were generally cooler, with a closer canopy and moister soil than SROAK plots. A Hill-Smith ordination performed on all measured leaves confirmed that the leaf economics spectrum is the main axis of trait correlation and also showed that legumes were separated from other species on the second axis (Appendix D).

Changes with succession – multi-trait approach

The RLQs (Fig. 1) showed strong links between sapling traits and environmental factors with 88.8% and 97.0% of the total cross-covariance explained by the first two axes of the between- and within-species RLQ, respectively. In both cases, most of the total cross-covariance was explained by the first axis (71.0% and 75.4% respectively). Most of the structure was explained by species turnover as shown by the higher eigenvalues of the between-species RLQ (3.55 and 0.89 for axes 1 and 2) compared with those of the within-species RLQ (0.48 and 0.14). The first axis of the between-species RLQ showed an association of conservative strategy (high LCC, density and LDMC) and legumes (with bipinnate leaves) with high temperature and canopy openness during the wet season at one end of the axis, and acquisitive strategies (high SLA) and moist soil at the other end. This axis also contrasted forest types, with SROAK having more conservative strategies and hotter and more open plots than SRTDF. The within-species RLQ showed a similar trend for the first axis, but with a larger contribution of leaf thickness at the conservative strategy end and of SLA and LNC at the acquisitive end. The second axis of the between-species RLQ contrasted saplings with deciduous and pubescent leaves in more open and hotter plots (as measured during the dry season) *versus* evergreen and glabrous ones in older successional plots. The second axis of the within-species RLQ was associated with leaf chemistry and soil properties.

(a) Between-species RLQ (species turnover)



(b) Within-species RLQ (intraspecific variation)

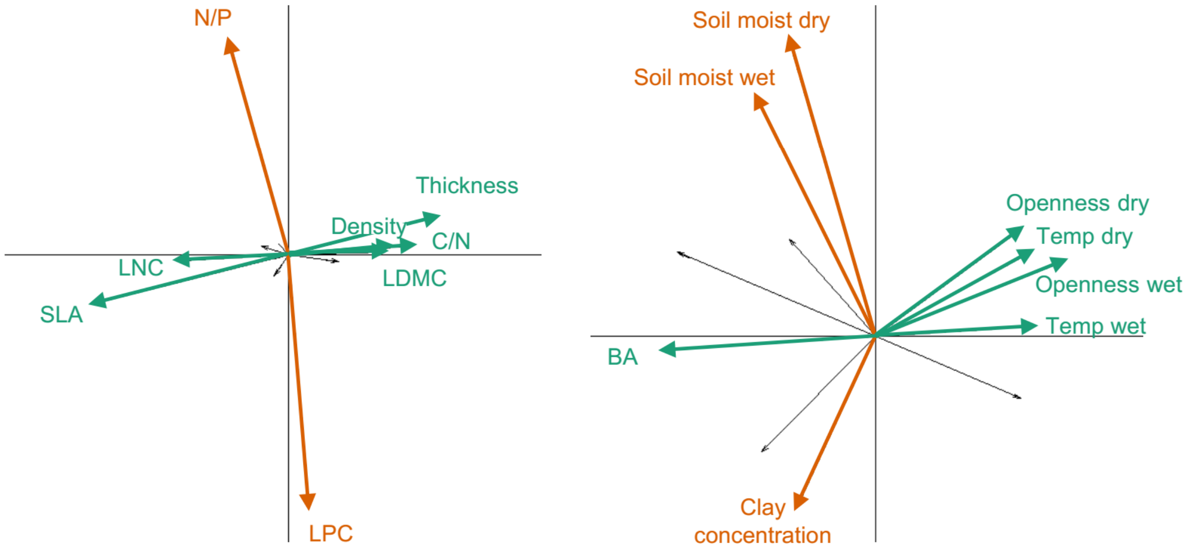


Figure 1. First factorial planes for (a) the between-species RLQ and (b) the within-species RLQ of the relationship between sapling leaf traits and environmental factors. For each partial RLQ, traits (left plot) and environmental factors (right plot) are presented in the same factorial plane but are plotted separately for ease of reading. The arrows represent the coefficients of each variable on the first two axes. Arrows pointing in the same direction therefore represents variables co-varying positively. The labels and arrows in color indicate traits that make at least 5% of the contribution of all traits to an axis and environmental factors that make at least 8% of the contribution of all environmental factors (green for axis 1 and orange for axis 2). These thresholds were chosen to display variables contributing more than average. 'Openness' stands for 'canopy openness', 'Temp.' for 'air temperature' and 'Soil moist' for soil moisture, and 'dry' and 'wet' indicate the season of measurement of these environmental factors.

Changes with succession – single-trait approach

The analyses conducted with the single-trait approach showed contrasting results for the two forest types, with more significant associations between community trait values and environmental factors in SRTDF than in SROAK (Table 1). Generally, the changes of community trait values with successional age correlated well with the leaf economics spectrum, trait values associated with conservative strategies decreasing (except for leaf density) and those associated with acquisitive strategies increasing with successional age. In SROAK, this trend was limited to SLA. The decrease in canopy openness was associated with a change in community trait values from acquisitive to conservative (increase in SLA and LPC and decrease in LCC) through ITV (Table 1). The associations with air temperature for the continuous traits were less clear and differed between the two forest types. Soil moisture was associated mainly with leaf chemical concentrations, while soil pH and clay concentration showed no significant association with community trait values. Species turnover generally had stronger contributions than ITV to the response of community trait values to environmental variation but more associations were significant for ITV (Table 1). For the significant trait-environment associations, species turnover and ITV generally led to changes in the same direction, with the exception of LDMC and leaf density.

Table 1. Contribution of species turnover only (Turn), intraspecific variation only (ITV) and their covariation (Covar) to the relationships between environmental factors and sapling community trait values.

Site	Trait	Successional age			Air temperature (dry season)			Canopy openness (wet season)			Soil moisture (dry season)		
		Turn	ITV	Covar	Turn	ITV	Covar	Turn	ITV	Covar	Turn	ITV	Covar
SRTDF	Thickness	12.4 (ns)	7.1 (.)	18.8	22.3 (ns)	3.9 (ns)	18.6	1.8 (ns)	6.2 (ns)	6.7	1.5 (ns)	0 (ns)	-0.5
	Petiole	1 (ns)	0.1 (ns)	-0.4	14 (ns)	0 (ns)	0.7	6.4 (ns)	0 (ns)	-1.1	3.3 (ns)	0.7 (ns)	-3
	LA	8.3 (ns)	1.7 (ns)	-7.5	17.4 (ns)	0.1 (ns)	-2.8	0.1 (ns)	0 (ns)	0	2.9 (ns)	4.2 (ns)	-7
	SLA	0.2 (ns)	**9.5 (*)**	2.5	14.6 (ns)	6.5 (ns)	19.5	0.1 (ns)	7.6 (.)	1.7	0.2 (ns)	0.3 (ns)	-0.5
	LDMC	30 (ns)	1 (ns)	-11	23.9 (ns)	2.2 (.)	-14.4	1.2 (ns)	1.2 (ns)	2.4	46.5 (ns)	0.5 (ns)	-9.5
	density	**75.1 (*)**	1.2 (ns)	-18.9	27.7 (ns)	3.5 (.)	-19.5	30.1 (ns)	1.8 (ns)	-14.7	19.6 (ns)	0.2 (ns)	-4.1
	LPC	7 (ns)	3.9 (ns)	10.5	11 (ns)	2.4 (ns)	10.3	10.5 (ns)	**7.1 (*)**	17.3	3.6 (ns)	0.9 (ns)	3.5
	LCC	4.4 (ns)	5 (ns)	-9.4	26.1 (ns)	0 (ns)	-2.2	6.4 (ns)	8.5 (.)	14.8	**58.5 (*)**	0.5 (ns)	10.5
	LNC	46.9 (.)	**2.4 (*)**	21.3	45.6 (.)	0.7 (ns)	11.3	9.8 (ns)	0.8 (ns)	5.7	9.4 (ns)	0.2 (ns)	2.5
	C/N	32.5 (ns)	**1.8 (*)**	15.3	39.9 (ns)	0.4 (ns)	8	1.7 (ns)	1 (ns)	2.6	12.7 (ns)	0 (ns)	-0.2
	N/P	**52.4 (*)**	0.1 (ns)	4.8	39.5 (.)	0 (ns)	-0.7	6.2 (ns)	0.8 (ns)	-4.6	37.7 (ns)	1.7 (ns)	16.1
SROAK	Thickness	0.5 (ns)	5.2 (ns)	-3.3	21.3 (ns)	1 (ns)	9	0.3 (ns)	5.1 (ns)	-2.4	1.2 (ns)	0.6 (ns)	1.7
	Petiole	3 (ns)	0.6 (ns)	-2.7	52.4 (.)	0.3 (ns)	-7.9	0.6 (ns)	0.7 (ns)	-1.3	22.5 (ns)	0.1 (ns)	-3.5
	LA	0 (ns)	0 (ns)	0	11.8 (ns)	0.2 (ns)	-2.9	0.2 (ns)	0 (ns)	0	23.1 (ns)	0.4 (ns)	6.1
	SLA	1.2 (ns)	11.2 (.)	7.4	6.3 (ns)	0.3 (ns)	-2.6	5.9 (ns)	**12.7 (*)**	17.3	13.4 (ns)	3.7 (ns)	14
	LDMC	0.3 (ns)	0.1 (ns)	0.3	51.2 (.)	0.1 (ns)	-4.7	2.6 (ns)	0.1 (ns)	1	3.6 (ns)	0.2 (ns)	1.7
	density	7.8 (ns)	0.6 (ns)	4.2	25.4 (ns)	0 (ns)	-1.5	11.5 (ns)	0.7 (ns)	5.6	4.5 (ns)	0.2 (ns)	1.8
	LPC	1.2 (ns)	1 (ns)	-2.2	13.9 (ns)	0.8 (ns)	-6.9	0 (ns)	1.7 (ns)	0.1	5.1 (ns)	**17.7 (*)**	19
	LCC	17.4 (ns)	0.1 (ns)	2.3	8.8 (ns)	0.1 (ns)	-1.6	19.1 (ns)	0.2 (ns)	3.6	1.9 (ns)	0.3 (ns)	-1.4
	LNC	8.7 (ns)	0.9 (ns)	-5.6	2.1 (ns)	0.2 (ns)	-1.2	4.5 (ns)	1 (ns)	-4.3	9.3 (ns)	0.1 (ns)	1.6
	C/N	12.3 (ns)	0.5 (ns)	-4.9	5.1 (ns)	1 (ns)	-4.5	6.5 (ns)	0.5 (ns)	-3.7	8.2 (ns)	0.1 (ns)	1.4
	N/P	1.8 (ns)	0.6 (ns)	2.1	2.4 (ns)	0.2 (ns)	-1.5	2 (ns)	1.1 (ns)	2.9	10 (ns)	**13.8 (*)**	23.5

The numbers are the percentage of the total variation in the trait value (i.e. total sum of squares of the specific mean) explained by the relationship between the environmental factor and the trait value, through the effect of Turn, ITV and Covar (respectively). Dark grey shading indicates that the community trait value is positively correlated with the environmental factor (and light grey shading that it is negatively correlated), for the Turn and ITV parts. The significance of the linear models for the part that is only due to Turn and ITV (respectively) is shown in parentheses (asterisk for $P = 0.01\text{-}0.05$ and dot for $P = 0.05\text{-}0.1$). Only cases with $P < 0.1$ are shaded, and bold when $P < 0.05$. None of the relationships with soil pH or clay concentration had $P < 0.1$ (results not presented).

For the traits that do not vary within species (leaf phenological habit, compoundness, pubescence and membership of the Fabaceae), we found a significant decrease in the proportion of saplings of deciduous species with increasing successional age and decreasing temperature, and a decrease in the proportion of saplings with pubescent leaves with decreasing temperature and canopy openness (for SRTDF) (Fig. 2).

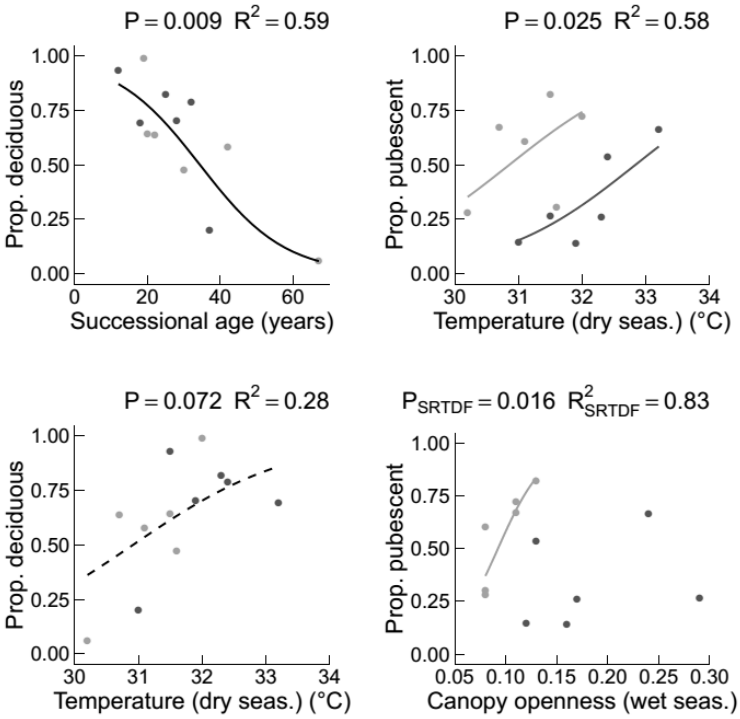


Figure 2. Models for the relationships between the sapling community values for categorical traits and environmental factors. 'Temperature' stands for 'air temperature', 'seas.' for season and 'prop.' for 'proportion'. Only the models with slope $P < 0.1$ are shown (solid line for $P < 0.05$, dashed line otherwise). The dots represent the observed values. Dark grey dots and lines are for the SROAK forest type, light grey ones for SRTDF and black lines are the relationships for which forest type is not kept in the best model.

Changes with ontogeny

Among the 11 traits measured within species, five showed significant correlations with ontogeny (Fig. 3): leaf thickness, density, LDMC and LCC increased with H/Hmax while SLA decreased, showing a change from acquisitive to conservative strategies with ontogeny. For leaf thickness, SLA and LCC, the direction of change was the same for all species, showing a consistent change of trait values with ontogeny across species. LDMC, and to a lesser extent leaf density, tended to decrease with ontogeny for species with high values and increase for species with low values (Appendix E), suggesting a greater differentiation of strategies in earlier ontogenic stages.

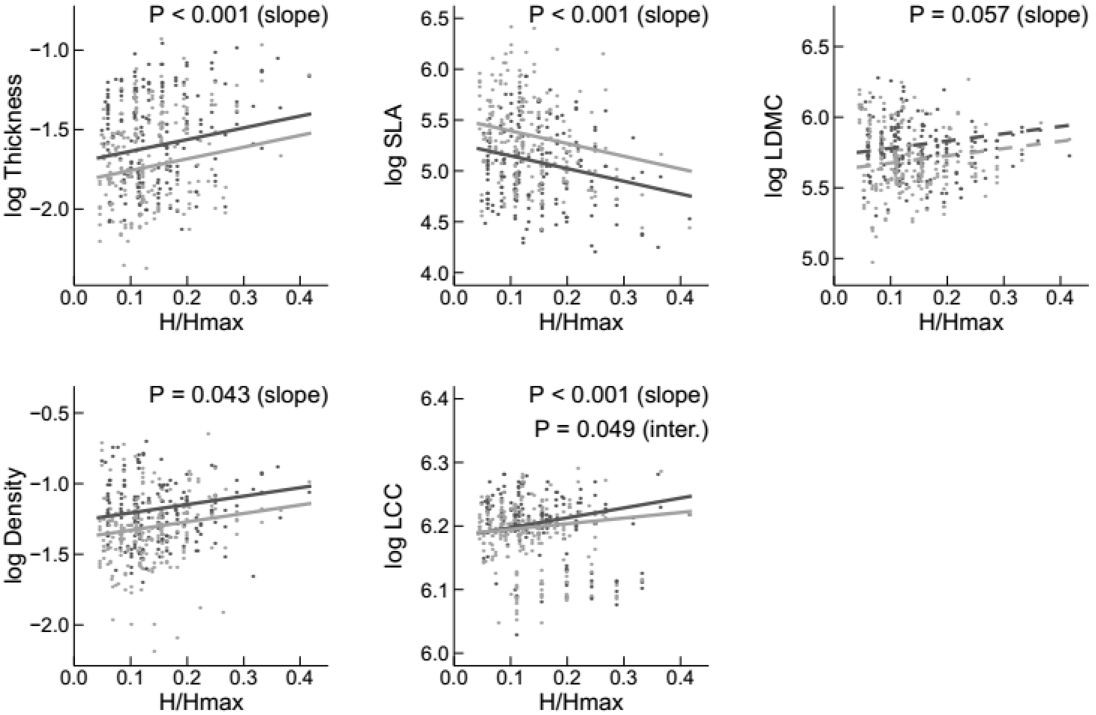


Figure 3. Selected models for the intraspecific trait variation with ontogeny (H/Hmax). Only the models with slope $P < 0.1$ are shown (solid line for $P < 0.05$, dashed line otherwise). ‘inter’ stands for ‘interaction’ (i.e. the interaction between H/Hmax and forest type). The lines represent the fitted models for all species and the dots the observed values. Dark grey dots and lines are for the SROAK forest type and light grey ones for SRTDF.

Discussion

While several recent studies have examined changes in leaf traits through secondary succession in both wet and dry tropical forests (Lebrija-Trejos et al. 2010, Lohbeck et al. 2013, Becknell and Powers 2014, Buzzard et al. 2015, Lohbeck et al. 2015), ours is the first to simultaneously evaluate the contributions of species turnover and ITV to these processes, and to compare the direction of changes with succession and ontogeny.

Changes of functional composition with succession

We found two main trends of changes in sapling community functional composition during succession: (1) a shift from conservative towards acquisitive strategies and a decrease in the proportion of legumes, which is by far the most important trend (as shown by the cross-covariance explained by the first axes in the RLQ). Both were associated with the changes in environmental conditions measured during the wet season. (2) There was a decrease in drought-coping strategies (deciduousness and pubescence) associated with the amelioration of environmental conditions during the dry season. These trends were consistent for the two analytical approaches, with the exception of changes in leaf density. The first trend suggests the importance of the wet season for resource acquisition and growth, with the dry season being more determinant for survival (Lebrija-Trejos et al. 2011). Conservative strategies were found in the more open and hot environment of early succession (Fig. 1 and Table 1). This result suggests that high temperature and irradiance limit photosynthesis more than low light, which is consistent with the results of Lebrija-Trejos et al. (2010). Conservative strategies reduce leaf heat and transpiration, allowing plants to endure the higher evaporative demand of open and hot environments, at the expense of resource acquisition (Lebrija-Trejos et al. 2010, Markesteijn et al. 2011). Legumes can maintain a high rate of biomass accumulation with a low rate of water use in these harsh environments because they have a lower proportion of sapwood and their compound-leaves favor convective cooling; many species also have a capacity to fix nitrogen (Poorter and Markesteijn 2008, Powers and Tiffin 2010, Reyes-Garcia et al. 2012). The second trend shows that survival during the dry season is favored by the drought-avoiding deciduous phenological habit (Poorter and Markesteijn 2008).

The trends that we observed are consistent with other studies of community weighted mean trait values carried out in Costa Rican TDF, but differ from studies conducted in Mexico. In Costa Rica, Becknell and Powers (2014) and Buzzard et al. (2015) found trends indicating a change from conservative to acquisitive strategies with succession (an increase in SLA and LNC, and an increase in SLA and LPC together with decrease in LDMC and C/N, respectively). However, in Mexican TDF, Lohbeck et al. (2013) found a decrease in SLA with succession, suggesting a reduction in acquisitive strategies, while Lebrija-Trejos et al. (2010) found a decrease in LDMC and density, suggesting a reduction in conservative strategies, but no association of SLA with succession. Moreover, Lohbeck et al. (2013, 2015) showed that the decrease in deciduousness and leaf compoundness was more important than the changes associated with the leaf economics spectrum in Mexican TDF. This can have two non-mutually exclusive explanations. (1) The lower annual precipitation in the studied Mexican TDF (900 mm) results in a greater relative importance of survival in the dry season than performance in the wet season for community assembly. (2) In Mexican TDF, deciduous species have been shown to have trait values associated with acquisitive strategies (Pringle et al. 2011) whereas there is a great overlap of trait values between deciduous and evergreen species in Costa Rican TDF (Powers and Tiffin 2010). The decrease in acquisitive trait values during succession in Mexican TDF could therefore be an indirect consequence of the reduced proportion of individuals of deciduous species.

Forest type had a strong influence on our results: the plots of SROAK were more dominated by saplings with conservative strategies and have more legume, pubescent, deciduous and compound-leaved individuals than the SRTDF plots (Appendix F). The association between community trait values and successional age, air temperature (dry season) and canopy openness (wet season) were weaker in SROAK (Table 1), although the decrease in SLA with succession was still observed. This result may be due to the overall higher temperature and more open canopy of the SROAK plots. It also suggests the importance of other factors driving community assembly in this forest type: the nutrient poor soil of oak forests (Appendix C, Waring et al. 2016) may be a stronger limitation than microclimatic conditions. Moreover, the chronosequence is shorter in SROAK (37 years versus 67 years in SRTDF), which may make directional changes in community trait values more difficult to observe.

Importance of intraspecific trait variation for community assembly

We found that the contribution of species turnover to the response of sapling communities to the change in environmental conditions during succession was more important than the contribution of ITV (Table 1 and eigenvalues of the partial RLQs). This could result from a combination of two explanations. (1) There is a high species turnover among plots in our study, as shown by relatively low Sørensen similarity indices between plots of different successional ages (mean 0.409 and range 0.222-0.615 in SROAK, and mean 0.335 and range 0.077-0.615 in SRTDF). (2) The interspecific variation of trait values is generally higher than their intraspecific variability, as shown by several studies in TDF (Markesteijn et al. 2007, Hulshof and Swenson 2010, Powers and Tiffin 2010). Nevertheless, the changes in community trait values through ITV are strongly associated with the changes in environmental conditions during succession, as shown by the high percentage of cross-covariance explained by the first axis of the within-species RLQ and the higher number of significant relationships between environmental factors and trait values for ITV than species turnover in Table 1. This result confirms that the directionality of changes in trait values within species along environmental gradients found in previous studies (Lepš et al. 2011, Bhaskar et al. 2014, Carlucci et al. 2015) is relevant in the context of successional gradients in TDF. ITV can allow species to establish in a wider range of environmental conditions, resulting in a greater niche overlap between species (Violle et al. 2012). This increased functional redundancy between species can increase the stochasticity of community taxonomic composition (Hubbell 2005). This supports the idea that the drivers of community assembly can be better understood by considering the functional composition of communities rather than their taxonomic composition (Messier et al. 2010).

Morphological and chemical traits associated with leaf economics (SLA, LPC, LNC and leaf thickness) showed a notable response of ITV to environmental changes (Fig. 1 and Table 1), suggesting a plastic response of these traits to environment. This result is consistent with previous studies of plant communities worldwide (Siefert et al. 2015) including those in temperate and tropical forests of responses to light, soil resources, topography and elevation (Markesteijn et al. 2007, Kichenin et al. 2013, Tomlinson et al. 2013, Carlucci et al. 2015, Kumordzi et al. 2015, Spasojevic et al. 2016).

The direction of change in community trait values in response to environmental changes that occur through ITV mirrors that through species turnover for most traits with a significant correlation, as shown by their positive covariations (Table 1). This result is in accord with the results of Carlucci et al. (2015) for light gradients in TDF. Environmental factors influence trait values in the same way across and within species and the effects of species-turnover and ITV reinforce each other (Lepš et al. 2011). However, for LDMC and leaf density, the covariations were either negative or very low (Table 1) showing opposed responses of species-turnover and ITV to succession. Such patterns have also been found in temperate forests and grasslands (Lepš et al. 2011, Kichenin et al. 2013, Kumordzi et al. 2015) but their physiological explanation is still uncertain. Further research is required to determine if, within TDF tree species, the values of some traits follow a bell-shaped curve along environmental gradients with a maximum at some optimal condition, as found by Albert et al. (2010) for LDMC in herbaceous and woody temperate species. This would lead to different directional changes in trait values between species depending on the extent of overlap between the sampled environmental gradient and the species' trait-value range. When scaled up to the community, this could explain the few cases where there is an opposite directions of change in community trait values through ITV and species turnover. Such negative covariation could also explain the opposite results observed for leaf density in the different approaches that we used (Fig. 1 and Table 1).

Our results on the contribution of ITV to the changes in community values with changing environmental conditions during succession support the importance of considering ITV in community assembly studies (Lepš et al. 2011, Violle et al. 2012, Shipley et al. 2016). In our study, calculating community means only on the basis of mean values per species across the chronosequences would have produced weaker evidence of a link between community trait values and environmental factors than we found (Table 1). For example, SLA, one of the most commonly studied traits, was only significantly correlated with environmental factors through changes within species and would not have been detected without including ITV.

Intraspecific changes due to ontogeny

Within species, we found directional changes of individual trait values with sapling ontogeny (indicated by H/Hmax) for five traits (Fig. 3), showing a trend from acquisitive to conservative strategies with tree size (increase in leaf thickness, density, LDMC and LCC and decrease in SLA). Because we sampled individuals in contrasting environmental conditions (*i.e.* with different access to light due to their different sizes and successional changes), this change could partly result from confounding phenotypic plasticity. However, the correlation of individual sapling H/Hmax with its crown illumination index is low (Kendal rank-order correlation, $Tau = 0.077$, $P = 0.033$), which suggests that instead ontogeny is a major cause of the intraspecific variation in the five traits. Such a change in resource acquisition strategies with ontogeny has been found in other biomes: a decrease in SLA from seedlings or saplings to adults or with increasing tree size has been frequently observed in temperate (Thomas and Winner 2002, Niklas and Cobb 2008, Sendall and Reich 2013, Spasojevic et al. 2014) and tropical moist forests (Poorter 2007). Thomas and Winner (2002) also observed an increase in leaf thickness, density and C concentration with ontogeny. Although the underlying mechanisms are still poorly understood (Niklas and Cobb 2008), Thomas and Winner (2002) proposed several hypotheses to explain this trend: (1) an increase in radiation, wind exposure and physical abrasion experienced by taller trees can result in both plastic responses and natural selection for more conservative strategies and (2) water transport limitation due to gravity can limit leaf extension in taller trees, leading to decreased SLA and increased leaf thickness.

If the changes that we observed for a short ontogenic window extend to the whole life of a plant from seedlings to adult trees, as suggested by the results from other forest biomes, then a tree growing in the successional TDF that we studied is likely to experience opposing changes due to succession (conservative to acquisitive) and ontogeny (acquisitive to conservative). This suggests that the interplay of changes due to succession and ontogeny may be more complicated in TDF than in tropical wet forests where these changes occur in the same direction. Our study cannot resolve the net outcome of these opposite changes because of the differing time scales of successional and ontogenic change. However, these opposing trends emphasize the importance of the choice of the ontogenetic stage considered when studying changes of community trait values. The wider range of values between species that we observed in the earlier ontogenic stages for LDMC and density support the importance of considering early ontogenic stages for understanding community assembly (Poorter 2007). Further studies considering the response of a wider range of ontogenic stages to environmental changes during succession in TDF are needed.

In conclusion, our results support the importance of considering both intraspecific variation and species turnover to understand community assembly along environmental gradients, especially given the indication of high plasticity of the traits associated with leaf economics. In the TDF that we studied, both species turnover and intraspecific variation contributed to a trend from conservative to acquisitive strategies with succession, but for some traits this change was more apparent for intraspecific variation. The opposite directional change of trait values with ontogeny that we found suggests that there could be an interplay between changes associated with environmental gradients and life stages that needs to be further studied.

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Supplemental material

Appendix A. Detailed methods for trait and environmental factor measurements

Appendix B. Mean values of leaf functional traits per species

Appendix C. Environmental factors measured for each forest type

Appendix D. Patterns of trait association

Appendix E. Selected models for the intraspecific trait variation with ontogeny

Appendix F. Mean of community trait values per forest type

Appendix A. Detailed methods for trait and environmental factor measurements.

Leaf trait measurements

Leaf traits were measured using standards protocols (Cornelissen et al. 2003, Perez-Harguindeguy et al. 2013). Three leaves were measured per individual except in the rare cases when the tree had an insufficient number of leaves. Because the saplings were in the understory, we did not measure sun leaves, but instead selected three leaves that were young, fully expanded with no visible damage and located in the upper part of the sapling crown. Twigs were collected in the early morning using a tree pruner, stored in vials filled with distilled water and placed in a cool bag for transportation to the laboratory. They were stored in a fridge and processed on the same day. We measured leaf fresh mass (g), leaf thickness (mm) and petiole length (mm), and visually determined leaf compoundness (simple, unipinnate and bipinnate) and leaf pubescence (binary) with a magnifier. Leaf area (LA, cm^2) was obtained by scanning the leaves and using the pixel counting software ImageJ (Abramoff et al. 2004). Leaves were then oven-dried at ~60 °C for at least 72 h and re-weighed. Specific leaf area (SLA, $cm^2 g^{-1}$) was calculated as LA/dry mass, leaf dry matter content (LDMC, mg g^{-1}) as dry mass/fresh mass and leaf density (g cm^3) as dry mass/(LA x thickness). Samples of 3 g of dried leaves composed of several leaves of each individual were shipped to Bangor University for chemical analyses. Leaves were ground in a mill. Leaf C (LCC, mg g^{-1}) and N (LNC, mg g^{-1}) concentration were measured in ~0.05 g of leaf matter by combustion analysis using a LECO Truspec CN Elemental Analyser (LECO corporation, Michigan, USA) calibrated with certified plant standards (Orchard Leaves Part No. 502-055, LECO corporation, Michigan USA). Leaf P concentration (LPC, mg g^{-1}) was measured by absorbance at 820 nm using a spectrophotometer (Epoch, Biotek, Vermont, USA) on ~0.2 g samples previously ashed at 500 °C and extracted in chloridric acid. We then calculated the stoichiometric ratios of C/N and N/P. All traits were measured on leaves including petiole and rachis because we considered them to be part of the leaf construction cost. The leaf phenological habit of each species was assigned to one of three categories (deciduous, semi-deciduous or evergreen) using data from Powers and Tiffin (2010) supplemented by information obtained from an expert on the local flora (D. Perez Avilez personal communication).

Measurement of environmental factors

Air temperature was measured with one data logger (i-button DS1921G, Maxim Integrated, California, USA) located in the centre of each plot at 50 cm above the soil surface. Measurements were taken simultaneously in all plots, every hour during 8 days and 11 days in the dry season (May) and in the wet season (July), respectively. The measurements taken between 5 am and 6 pm were averaged to give the mean diurnal air temperature for each season. To estimate light conditions, we used 10 hemispherical photographs taken every 5 m on the central line of each plot in the dry season (April) and in the wet season (July). The photographs were taken at 1.5 m above the soil surface using a Nikon Coolpix 4500 camera with a fish-eye lens mounted on a tripod following standard protocols (Newton 2007). They were analysed with the software HEMIv9 (Delta-T Devices, Cambridge, UK) and the values for the 10 photographs averaged to give the canopy openness (proportion of visible sky) for each season. Soil moisture was measured in the dry (May) and the wet season (November) with two measurements at eight locations within each plot, at a depth of 10 cm, using a soil moisture sensor (SM150-UM-1, Delta-T Devices, Cambridge, UK) and averaged to give one value per plot per season.

The soil physical and chemical variable values were taken from a previous study (Powers et al. 2009). In brief, bulk density and soil elemental concentrations were obtained from volumetric samples, soil pH was measured in water and percentages of sand, silt and clay were determined with the hydrometer method. Total elemental concentrations of Al, B, Ca, Cr, Cu, Fe, K, Mg, Mn, Na, Ni, P and Zn were quantified with inductively coupled plasma emission spectroscopy. Total C and N were measured with a COSTECH Elemental Analyzer (Costech Analytical Technologies, California, USA).

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Appendix B. Mean values of leaf functional traits per species. The number in parenthesis after the species name are the number of sampled individuals.

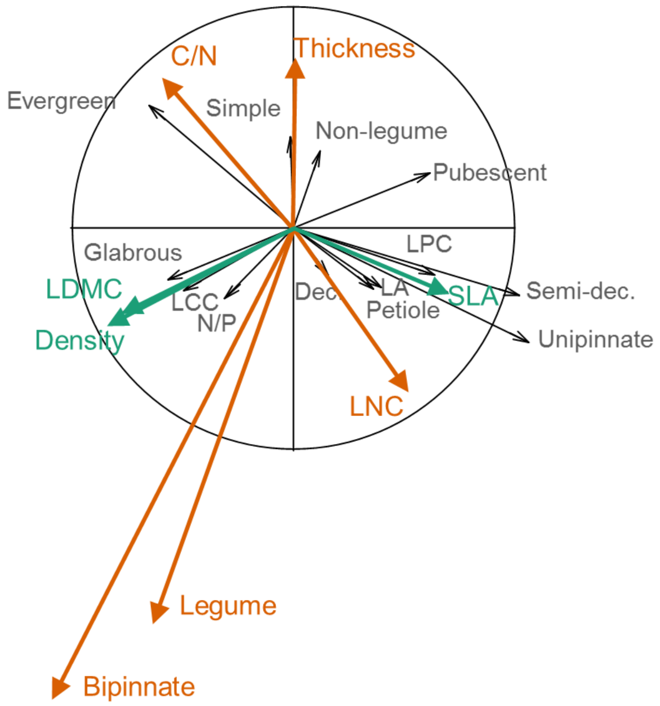
Species	Family	Thick-ness (mm)	Petiole lenght (mm)	Compoundness	Pubescence	LA (cm^2)	SLA ($cm^2 g^{-1}$)	LDMC ($mg g^{-1}$)	Density ($g cm^{-3}$)	Phenological habit	LPC ($mg g^{-1}$)	LCC ($mg g^{-1}$)	LNC ($mg g^{-1}$)	C/N	N/P
Acacia collinsii (101)	Fabaceae (Mimos.)	0.105	20.85	bipennate	No	67.563	182.778	480.11	0.57	deciduous	1.24	518.82	28.08	18.75	24.82
Acosmium panamense (3)	Fabaceae (Papilio.)	0.162	25.81	unipennate	No	107.783	230.612	319.93	0.27	semi-dec.	1.09	518.00	32.28	16.24	30.38
Alibertia edulis (76)	Rubiaceae	0.204	5.60	simple	No	37.711	125.423	365.84	0.41	evergreen	1.06	530.45	15.50	35.05	16.73
Alophyllus occidentalis (4)	Sapindaceae	0.209	54.68	unipennate	Yes	119.578	222.707	281.11	0.22	deciduous	1.93	490.75	36.15	14.11	19.49
Ardisia revoluta (20)	Primulaceae	0.286	7.78	simple	No	78.593	126.112	266.56	0.30	evergreen	1.35	495.95	12.88	39.33	10.40
Ateleia herbert-smithii (1)	Fabaceae (Papilio.)	0.161	52.32	unipennate	Yes	146.742	197.364	273.84	0.32	deciduous	1.35	517.00	32.85	15.74	24.35
Bauhinia ungulata (9)	Fabaceae (Caesalp.)	0.158	11.55	simple	Yes	23.956	213.716	433.41	0.31	deciduous	1.40	537.11	26.93	20.26	19.96
Bursera simarouba (17)	Burseraceae	0.195	110.53	unipennate	Yes	318.772	213.091	232.33	0.25	deciduous	1.43	475.76	23.01	20.96	16.74
Bursera tomentosa (25)	Burseraceae	0.193	42.05	unipennate	Yes	98.903	222.610	290.07	0.26	deciduous	1.31	498.52	18.55	27.30	16.28
Calycophyllum candidissimum (4)	Rubiaceae	0.173	5.80	simple	Yes	50.236	318.692	179.09	0.20	deciduous	1.42	482.75	19.62	24.80	13.77
Capparis frondosa (9)	Capparaceae	0.175	32.11	simple	No	82.089	127.803	442.12	0.45	evergreen	0.73	478.78	30.36	15.88	45.93
Capparis indica (5)	Capparaceae	0.239	7.49	simple	No	31.934	102.254	416.68	0.43	evergreen	0.70	454.60	33.13	13.98	56.38
Casearia arguta (1)	Salicaceae	0.137	2.46	simple	No	30.206	280.265	282.00	0.26	deciduous	1.41	485.00	23.46	20.68	16.67
Casearia corymbosa (13)	Salicaceae	0.149	2.23	simple	No	46.594	212.934	297.36	0.33	deciduous	1.74	485.00	26.01	18.98	15.82
Casearia sylvestris (10)	Salicaceae	0.150	3.13	simple	No	17.054	186.192	357.78	0.37	evergreen	1.30	497.00	30.66	16.98	24.49
Castilla elastica (13)	Moraceae	0.144	8.89	simple	Yes	161.371	488.066	221.65	0.15	semi-dec.	2.55	463.77	42.43	11.01	16.93
Chomelia spinosa (1)	Rubiaceae	0.169	7.50	simple	Yes	27.446	249.634	243.39	0.24	deciduous	1.08	517.00	25.77	20.07	23.89
Cochlospermum vitifolium (14)	Bixaceae	0.155	169.23	simple	Yes	154.852	171.641	280.31	0.39	deciduous	1.46	522.79	21.09	25.07	15.89
Cordia gerascanthus (3)	Boraginaceae	0.184	11.55	simple	Yes	50.842	236.760	240.92	0.23	deciduous	1.46	441.00	27.18	16.53	18.59
Cordia panamensis (3)	Boraginaceae	0.226	11.92	simple	Yes	140.469	200.219	368.46	0.24	deciduous	1.42	466.67	24.07	19.52	18.43
Cornutia grandifolia (1)	Lamiaceae	0.182	2.74	simple	Yes	49.408	308.369	188.35	0.18	deciduous	2.07	495.00	35.10	14.10	16.97
Crescentia alata (1)	Bignoniaceae	0.208	85.30	unipennate	No	22.585	186.914	298.98	0.26	semi-dec.	1.37	485.00	27.43	17.68	20.05
Dilodendron costaricense (1)	Sapindaceae	0.120	85.69	bipennate	Yes	421.057	173.939	474.04	0.49	deciduous	0.95	541.00	18.02	30.03	18.93
Diospyros salicifolia (11)	Ebenaceae	0.206	4.71	simple	Yes	27.172	143.419	388.04	0.36	deciduous	1.24	487.73	19.31	25.70	17.30
Erythroxylum havanense (17)	Erythroxylaceae	0.185	2.71	simple	No	13.793	197.601	355.85	0.28	deciduous	1.26	481.76	27.94	17.30	22.73
Eugenia monticola (7)	Myrtaceae	0.180	2.26	simple	No	5.792	194.534	333.50	0.29	deciduous	1.39	536.43	19.44	27.63	15.09
Eugenia salamensis (1)	Myrtaceae	0.217	2.05	simple	Yes	135.639	139.735	357.14	0.33	deciduous	1.45	517.00	14.94	34.62	10.33
Euphorbia schlechtendalii (19)	Euphorbiaceae	0.140	18.18	simple	No	3.602	345.826	257.80	0.22	deciduous	2.26	506.95	22.73	22.58	10.33
Genipa americana (5)	Rubiaceae	0.212	4.62	simple	Yes	566.290	159.599	299.39	0.30	deciduous	1.22	505.60	21.02	24.41	17.51
Gliricidia sepium (10)	Fabaceae (Papilio.)	0.227	28.70	unipennate	Yes	142.908	183.376	228.63	0.25	deciduous	1.79	505.10	33.61	15.08	19.66
Guazuma ulmifolia (4)	Sterculiaceae	0.146	10.14	simple	Yes	35.019	333.078	255.00	0.21	deciduous	1.36	475.00	25.95	18.82	19.46
Guettarda macrosperma (14)	Rubiaceae	0.142	12.17	simple	Yes	44.818	330.995	270.56	0.24	deciduous	1.16	486.21	23.05	21.71	21.05
Haematoxylum brasiletto (8)	Fabaceae (Caesalp.)	0.139	4.30	simple	No	3.391	235.927	357.99	0.32	deciduous	1.48	509.38	22.29	23.24	17.69
Hirtella racemosa (39)	Chrysobalanaceae	0.157	2.48	simple	No	14.128	149.284	468.53	0.45	evergreen	0.77	493.87	13.30	37.44	19.32
Jacquinia nervosa (2)	Primulaceae	0.282	4.47	simple	No	7.809	90.654	431.80	0.40	deciduous	0.21	503.00	11.00	47.16	53.98
Karwinskia calderonii (1)	Rhamnaceae	0.148	4.93	simple	No	7.474	224.427	404.13	0.31	deciduous	1.42	510.00	25.00	20.40	17.59
Lonchocarpus minimiflorus (4)	Fabaceae (Papilio.)	0.183	20.49	unipennate	Yes	54.405	210.065	358.23	0.28	deciduous	1.32	458.00	30.35	15.37	24.92
Lonchocarpus rugosus (4)	Fabaceae (Papilio.)	0.169	38.01	unipennate	Yes	130.420	234.619	365.92	0.26	semi-dec.	1.36	503.25	29.93	17.09	22.78

Species	Family	Thickness (mm)	Petiole lenght (mm)	Compoundness	Pubescence	LA (cm^2)	SLA (cm^2 g^{-1})	LDMC (mg g^{-1})	Density (g cm^{-3})	Phenological habit	LPC (mg g^{-1})	LCC (mg g^{-1})	LNC (mg g^{-1})	C/N	N/P
Luehea candida (17)	Malvaceae	0.163	4.20	simple	Yes	75.304	379.104	324.29	0.18	semi-dec.	2.01	500.18	26.07	19.95	13.14
Luehea speciosa (24)	Malvaceae	0.162	3.80	simple	Yes	47.935	270.642	422.62	0.24	semi-dec.	1.43	500.38	27.22	18.62	20.03
Mabea occidentalis (2)	Euphorbiaceae	0.162	6.77	simple	Yes	15.709	134.664	436.56	0.47	evergreen	1.68	548.00	22.19	24.70	13.25
Machaerium biovulatum (4)	Fabaceae (Papilio.)	0.139	36.27	unipennate	Yes	122.095	201.581	405.79	0.36	deciduous	1.22	490.50	28.33	17.36	24.24
Malvaviscus arboreus (26)	Malvaceae	0.231	46.37	simple	Yes	77.501	283.427	195.13	0.16	evergreen	1.66	409.50	29.69	14.30	18.44
Manilkara chicle (11)	Sapotaceae	0.216	16.40	simple	No	90.120	103.807	428.14	0.45	evergreen	0.63	510.27	15.72	33.07	28.71
Margaritaria nobilis (3)	Phyllanthaceae	0.149	3.29	simple	Yes	42.572	354.351	218.63	0.19	deciduous	1.76	472.67	32.41	14.72	18.42
Maytenus segoviarum (5)	Celastraceae	0.278	4.98	simple	No	23.376	92.268	411.21	0.40	semi-dec.	1.02	536.60	13.19	40.93	13.35
Mouriri myrtilloides (7)	Melastomataceae	0.175	1.11	simple	No	9.232	122.793	458.76	0.49	evergreen	0.72	500.14	14.86	33.94	24.28
Myconia argentea (2)	Melastomataceae	0.224	63.32	simple	Yes	187.228	113.490	335.75	0.40	evergreen	0.84	471.50	20.46	23.06	24.53
Myrospermum frutescens (3)	Fabaceae (Papilio.)	0.108	15.39	unipennate	No	60.955	346.173	268.76	0.27	deciduous	2.10	504.67	30.69	16.65	14.73
Ocotea veraguensis (11)	Lauraceae	0.155	6.82	simple	No	24.017	178.808	417.11	0.37	evergreen	1.02	529.73	28.49	18.72	29.64
Pithecellobium dulce (1)	Fabaceae (Mimos.)	0.201	18.67	bipennate	No	21.719	161.291	346.26	0.31	semi-dec.	1.61	476.00	33.34	14.28	20.76
Quercus oleoides (4)	Fagaceae	0.270	3.53	simple	Yes	22.791	83.723	493.80	0.45	evergreen	0.95	522.25	15.76	33.45	19.11
Randia monantha (16)	Rubiaceae	0.179	8.21	simple	Yes	27.747	267.136	293.91	0.22	deciduous	0.88	463.44	23.79	19.63	29.16
Rehdera trinervis (84)	Verbenaceae	0.261	6.43	simple	Yes	28.080	144.616	322.89	0.28	deciduous	1.05	501.71	17.23	29.60	18.83
Roupala montana (1)	Proteaceae	0.231	23.91	unipennate	No	54.697	83.213	558.57	0.53	semi-dec.	0.35	539.00	11.29	47.75	31.92
Sapindus saponaria (5)	Sapindaceae	0.178	25.86	unipennate	No	345.621	177.433	277.62	0.33	evergreen	2.70	512.20	33.87	15.64	13.16
Schoepfia schreberi (1)	Schoepfiaceae	0.262	2.79	simple	No	13.842	130.001	289.41	0.29	evergreen	1.75	459.00	17.62	26.05	10.04
Sebastiania pavoniana (37)	Euphorbiaceae	0.146	6.58	simple	No	30.969	277.146	283.14	0.26	deciduous	1.99	489.76	24.08	20.56	13.26
Semialarium mexicanum (66)	Celastraceae	0.261	3.19	simple	Yes	29.732	135.024	294.47	0.30	deciduous	1.15	447.18	16.02	28.31	15.08
Simarouba glauca (3)	Simaroubaceae	0.228	71.18	unipennate	Yes	212.942	155.077	344.45	0.31	evergreen	1.03	491.00	20.12	26.02	21.89
Sloanea terniflora (2)	Elaeocarpaceae	0.170	8.42	simple	No	33.977	126.129	506.22	0.47	evergreen	0.77	500.50	13.85	36.57	18.54
Spondias monbin (2)	Anacardiaceae	0.234	46.37	unipennate	No	179.375	208.947	211.77	0.22	deciduous	1.67	473.00	22.47	21.33	16.15
Stemmadenia obovata (1)	Apocynaceae	0.173	4.50	simple	Yes	141.603	344.964	171.30	0.17	deciduous	1.96	482.00	36.15	13.33	18.42
Swietenia macrophylla (2)	Meliaceae	0.151	74.57	unipennate	No	269.822	189.832	350.81	0.36	deciduous	0.84	496.50	18.49	26.87	24.37
Tabebuia ochracea (17)	Bignoniaceae	0.166	147.72	unipennate	Yes	417.076	216.145	373.81	0.30	deciduous	1.94	495.82	37.39	13.40	19.88
Tabebuia rosea (7)	Bignoniaceae	0.192	145.44	unipennate	No	407.550	174.315	266.36	0.32	deciduous	1.75	488.57	21.59	22.95	12.84
Trophis racemosa (1)	Moraceae	0.161	5.50	simple	No	44.101	235.109	356.94	0.27	evergreen	1.29	465.00	23.17	20.07	18.01
Xylosma flexuosa (4)	Salicaceae	0.226	1.52	simple	No	9.723	115.393	419.94	0.41	evergreen	0.84	483.25	12.85	37.69	16.49
Zuelania guidonia (2)	Salicaceae	0.206	6.48	simple	Yes	75.134	198.590	330.98	0.25	deciduous	1.36	507.50	22.75	23.28	17.77
	Minimum	0.105	1.11	NA	NA	3.391	83.213	171.30	0.15	NA	0.21	409.50	11.00	11.01	10.04
	Maximum	0.286	169.23	NA	NA	566.290	488.066	558.57	0.53	NA	2.70	548.00	42.43	47.75	56.38

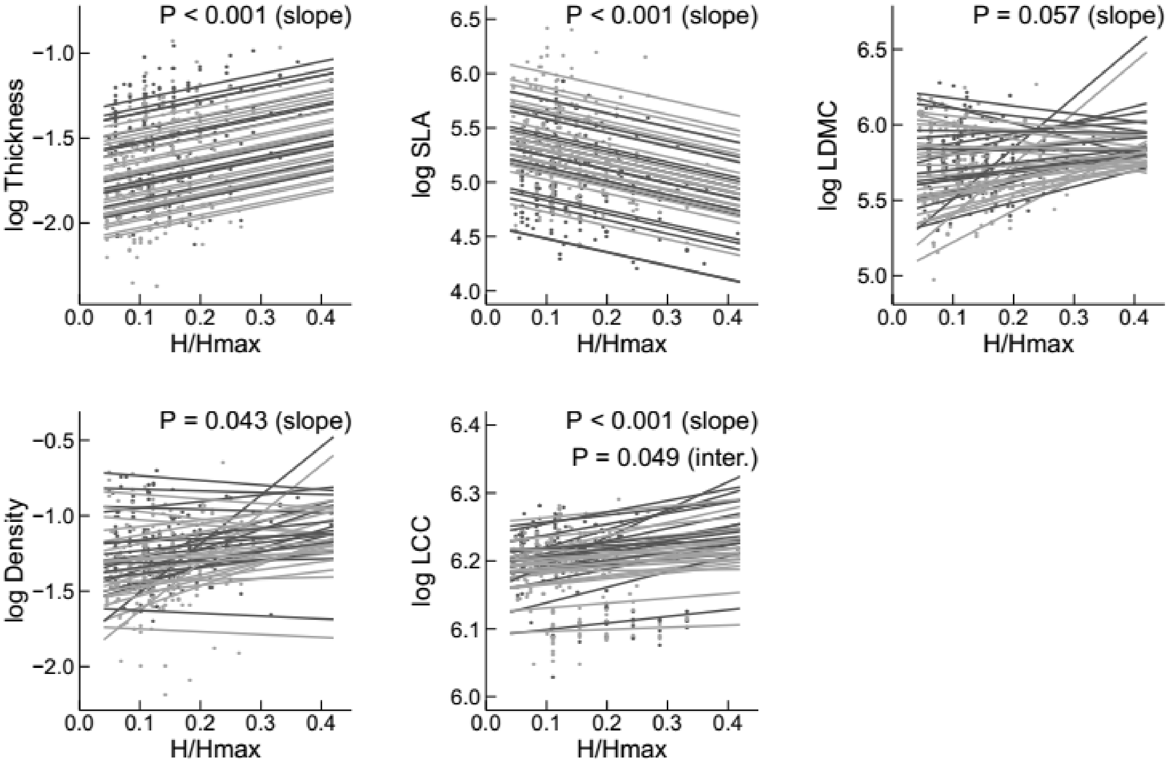
Appendix C. Environmental factors measured for each forest type. For correlation with successional age, the first number is the Pearson coefficient; *P*-values are given in brackets. Correlations significant at $P < 0.05$ are given in bold.

	for forest type SRTDF		for forest type SROAK	
	Mean (range)	Correlation with successional age	Mean (range)	Correlation with successional age
Successional age (years)	33.3 (19-67)		25.3 (12-37)	
Basal area (m^2 ha^{-1})	18.9 (13.0-27.2)	0.30 (0.566)	12.5 (5.3-20.3)	0.70 (0.122)
Air temperature (dry season) (°C)	31.2 (30.2-32.0)	-0.75 (0.087)	32.0 (31.0-33.2)	-0.33 (0.526)
Air temperature (wet season) (°C)	28.5 (27.9-29.2)	-0.61 (0.200)	29.7 (29.0-30.3)	-0.76 (0.082)
Canopy openness (dry season) (prop.)	0.32 (0.14-0.49)	**-0.90 (0.016)**	0.36 (0.14-0.53)	**-0.84 (0.037)**
Canopy openness (wet season) (prop.)	0.10 (0.08-0.13)	-0.72 (0.105)	0.18 (0.12-0.29)	**-0.98 (0.001)**
Soil moisture (dry season) (% vol)	19.5 (17.1-22.4)	0.32 (0.531)	13.0 (5.2-19.4)	-0.55 (0.260)
Soil moisture (wet season) (% vol)	32.4 (30.6-35.0)	0.51 (0.305)	24.1 (16.8-30.1)	-0.28 (0.585)
Soil pH	6.1 (5.7-6.7)	-0.37 (0.473)	5.8 (5.7-6.1)	-0.20 (0.706)
Soil stone content (g cm^{-3})	0.008 (0.003-0.012)	0.56 (0.253)	0.089 (0.007-0.327)	-0.41 (0.421)
Soil bulk density (g cm^{-3})	0.91 (0.85-1.03)	-0.30 (0.563)	0.80 (0.58-1.06)	0.26 (0.616)
Soil sand concentration (%)	40.0 (35.1-47.3)	0.01 (0.987)	44.4 (32.6-56.7)	0.50 (0.316)
Soil clay concentration (%)	31.8 (30.5-35.3)	-0.12 (0.815)	25.0 (16.7-33.4)	-0.34 (0.511)
Soil silt concentration (%)	28.2 (22.0-34.3)	0.04 (0.937)	30.5 (23.6-41.1)	-0.37 (0.471)
Soil Al concentration (ppm)	47709 (37940-58550)	**-0.84 (0.038)**	47319 (41671-59503)	-0.27 (0.610)
Soil B concentration (ppm)	19 (13-26)	-0.42 (0.412)	18 (15-20)	-0.04 (0.938)
Soil Ca concentration (ppm)	7332 (4185-15248)	-0.31 (0.555)	4842 (1932-6337)	0.17 (0.742)
Soil Cr concentration (ppm)	17 (6-56)	-0.09 (0.863)	10 (8-15)	-0.23 (0.657)
Soil Cu concentration (ppm)	65 (44-114)	-0.39 (0.444)	50 (36-66)	-0.01 (0.981)
Soil Fe concentration (ppm)	33359 (22819-40040)	-0.66 (0.150)	32511 (24211-41916)	-0.43 (0.401)
Soil K concentration (ppm)	1205 (440-3731)	-0.20 (0.698)	512 (386-630)	-0.35 (0.497)
Soil Mg concentration (ppm)	2840 (972-9939)	-0.17 (0.745)	1206 (825-1926)	0.16 (0.768)
Soil Mn concentration (ppm)	762 (366-1590)	-0.49 (0.321)	620 (208-1262)	-0.55 (0.256)
Soil Na concentration (ppm)	719 (516-913)	-0.23 (0.657)	739 (238-1204)	0.35 (0.492)
Soil Ni concentration (ppm)	15 (5-49)	-0.09 (0.864)	35 (9-149)	-0.38 (0.455)
Soil P concentration (ppm)	378 (124-1272)	-0.19 (0.715)	108 (31-213)	0.22 (0.682)
Soil Zn concentration (ppm)	54 (27-69)	-0.67 (0.145)	33 (19-51)	-0.43 (0.400)
Soil N concentration (ppm)	0.31 (0.27-0.38)	0.38 (0.456)	0.24 (0.19-0.28)	0.12 (0.817)

Appendix D. Patterns of leaf trait association. Correlation circle for the Hill and Smith analysis (performed on 2536 leaves belonging to 851 saplings of 69 species) in the first factorial plane. The labels and arrows in colour indicate variables that contribute at least 10% of the inertia of an axis (green for axis 1 and orange for axis 2). Axes 1 and 2 explain respectively 25.23% and 22.24% of the total inertia. *Dec.* is deciduous.



Appendix E. Selected models for the intraspecific leaf trait variation with ontogeny (H/Hmax) (performed on 420 individual saplings of 26 species). Only the models for which the slope *P*-value is < 0.1 are presented (solid line for *P* < 0.05, dashed line otherwise). 'inter' stands for 'interaction' (i.e. the interaction between H/Hmax and forest type). The lines represent the fitted models per species and the dots the observed values. Dark grey dots and lines are for the SROAK forest type and light grey ones for SRTDF.



Appendix F. Mean community leaf trait values per forest type (calculated with the value for each individuals of a plot)

Forest type	SROAK	SRTDF
Leaf thickness (mm)	0.175	0.186
Petiole length (mm)	19.88	22.35
Leaf area (cm^2)	58.685	92.618
Specific Leaf Area (cm^2 g^{-1})	170.630	230.177
Leaf Dry Matter Content (mg g^{-1})	392.68	311.93
Leaf density (g cm^{-3})	0.41	0.28
Leaf Phosphorous Concentration (mg g^{-1})	1.26	1.37
Leaf Carbon Concentration (mg g^{-1})	507.31	480.50
Leaf Nitrogen Concentration (mg g^{-1})	21.66	25.45
Leaf C/N ratio	25.87	20.99
Leaf N/P ratio	19.55	21.03
Proportion of simple-leaves individuals	0.633	0.795
Proportion of pubescent individuals	0.335	0.567
Proportion of deciduous individuals	0.690	0.563
Proportion of legume individuals	0.329	0.066